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STUDIES ON NORTH AMERICAN CERCARIAE

WITH EIGHT PLATES

By

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I. INTRODUCTION*

From the time of Joseph Leidy to comparatively recent years American larval trematodes and trematode life histories have received increasing attention. Before Cort published his pioneer work on larval trematodes of Illinois, very little was known about these larvae in North America, and even in Europe only a few life cycles were known. Up to 1914 only twelve cercariae had been reported from North America, but in the same year Cort added fourteen new species to this list.

Faust described fifteen additional species in 1917 and two years later compiled a list of eighty-one described forms from the United States. Such studies became more prevalent soon after this time, so that McCoy in 1928 estimated the number of described cercariae in this country as about one hundred, but stated that the complete life histories of only four trematodes in the United States were known. Up to 1929 ten complete life histories had been described.

While these estimates may in some cases be incomplete, nevertheless they serve to show one of the trends of modern investigation in the field of Helminthology. Now the number of described cercariae in this country has reached such proportions that it is not practical even to refer to all previous descriptions in this paper. Descriptions from the state of Illinois alone, including those in the present paper, cover thirty-eight species.

In some attempts to establish life histories of these forms, either experimentally or morphologically, many errors have occurred, largely because of unsubstantiated generalizations or insufficient experimentation. Due to a diversity of structure within each of the several larval groups, I find many difficulties are encountered in determining a relationship between the morphology and the developmental cycle. In short, I believe Dollfus (1914) was right when he stated that cercariae very similar in structure dwell in different hosts and have very different kinds of development, and that cercariae very different morphologically live in identical environments and have similar courses of development.

In his classification of cercariae in 1909, Lühe recognized five major groups, Lophocercariae and Gasterostome, Monostome, Amphistome, and Distome Cercariae. He further subdivided the Distome Cercariae into the Cystocercous, Rhopalocercous, Leptocercous, Trichocercous, Furcocercous, Microcercous, and Gorgonocephalous Cercariae, as well as tailless cercariae.

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*It is not convenient to consider here several publications which have appeared since this manuscript was completed in 1934.

Lebour (1912) used the development in sporocysts or rediae of these forms as a basic factor in her scheme of classification. Viewing this plan now in the light of numerous additions to taxonomic lists of cercariae from various parts of the world, I realize that such a scheme can denote only very general relationships since individuals of the subgroups within each of these two large groups differ greatly in most other respects.

No one can doubt that an accurate classification of cercariae based purely on relationship would be of great value in indicating possible clues to the life histories of closely related larvae. However, the still inadequate knowledge concerning the value of many larval characters in revealing adult relationships and the inadequate descriptions of many cercariae make such a classification still impossible for all of the described larvae.

Certain larval structures, such as the number and position of the penetration glands, the shape of the bladder, the branching of the excretory system, the shape and size of the stylet, and the character of the germinal mass, should be regarded as less important for definite specific diagnoses and more important for showing subgroup relationships. Earlier workers were sometimes inclined to regard these characters as specific.

Perhaps the statement of Faust (1917) shows adequately the viewpoint taken by some more recent workers, when he says: "The writer has attacked this part of the problem with the idea in mind that not only the fundamentals of the adult trematode are found in the mature cercaria, but that even the main descriptive features of the adult trematode are already present, so that the worker can recognize the adult in the larva." After various studies on many cercariae I am inclined to depart somewhat from the above viewpoint, for while many of the larval characters resemble closely those of the adult, yet I find several incompletely developed structures in the cercaria which bear little resemblance to the same structures in the adult. For instance, the poorly defined and shapeless germinal mass of the emerged furcocercous cercaria bears little resemblance to the reproductive organs of the adult trematode. The character of the excretory system may change due to the division of the flame cells and the growth of tubules and capillaries, and even a ventral sucker may appear during the metacercarial stage (McCoy, 1929). I believe the above facts must be considered carefully if we are to progress toward the use of dependable characters of the cercaria for specific diagnosis.

Similarity between excretory systems has proved to be of great value in determining relationships but I find this similarity too great to have the systematic significance given it by some workers. Several instances of different species of cercariae, as well as different species of

adults, are on record in which the excretory systems are identical as to the arrangements of the tubules and terminal cells.

The discovery that many cercariae do not have the host-specificity originally supposed has brought to light almost identical descriptions of forms from different molluscan hosts.

The following studies may help in clarifying some of the earlier errors in taxonomy and descriptions of North American cercariae, and will add to the information concerning the life histories of several forms. Descriptions of four new cercariae are included in the morphological section of this paper, and I have added to the knowledge of nineteen additional species.

It is hoped that the survey of the Illinois forms and the summary of the localities and hosts from which each form has been reported may be of use to future investigators.

II. METHODS OF INVESTIGATION

Former workers who have placed emphasis on the study of living forms have recognized the advantages in such methods. Earlier descriptions of cercariae based on preserved and mounted material are responsible for much of the confusion existing in the literature at present. Such descriptions have made it impossible to determine the identity of many such forms with certainty and have made their inclusion in identification keys and systems of classification highly problematical.

As pointed out in my earlier paper (1930), technique methods do not insure a similarity in the proportions of body structures before and after killing and fixing. Obviously the study of such material cannot give a true and complete concept of these forms.

For these reasons the great majority of my investigations have been based on living specimens, and detailed studies of all forms included here have been made on the living animals with the aid of an oil immersion. Pressure of the cover slip is advantageous since it makes structures more visible. It also slows down the activity of the worm so that more accurate measurements can be completed on the living form. Most of the following observations were made on living cercariae under uniform pressure which was just strong enough to prevent rapid movement.

Measurements without explanations of the stages of contraction or expansion of the body mean very little. Therefore I have tried particularly to obtain measurements at various stages of body contraction and extension. Only in this way can such measurements be of use to future investigators. Abundant material for the study of local forms has made

this possible. All measurements mentioned here, unless otherwise specified, were made from living material, and represent the averages for at least five different individuals.

Recent workers have shown the error in basing descriptions on only partially developed cercariae which have been secured by dissection of the molluscan host. The following morphological studies have been made from cercariae after emergence from the mollusks. However, Stunkard (1930) has found that cercariae may leave the sporocyst or redia while still immature, and complete their development in the lymph spaces of the mollusk. My own observations have corroborated this, and, in addition, there is evidence that at least some of the stylet cercariae, under conditions of high temperature in small pools during the hot summer months, emerge from the snail prematurely. In such cases there are several points of difference between their structure and that of forms which emerge during the colder fall and spring days. It has been suggested in recent descriptions (Beaver, 1929; Horsfall, 1930) that some earlier descriptions have been based on such immature forms.

It would seem that abnormal conditions as yet little understood are at work, when observations show that at least with some species, those leaving the snail soon after it has been placed in a laboratory aquarium encyst normally, but those appearing later due to this artificial rise in temperature die without encysting. Perhaps their development has been speeded to such an extent that they break from the sporocyst and emerge from the snail prematurely, death consequently resulting. This may also explain why many hosts remain uninfected during the experimental life history studies of cercariae.

As indicated in the tables of collection records and in the collection dates in the description of each species included in this paper, my work extended over the period from September, 1931, to July, 1933. In the laboratory the snails were isolated in small vials or bottles and examined repeatedly for about forty-eight hours. Those not giving off cercariae were later examined for infections so that the rediae or sporocysts and developing cercariae might be studied. Infected individuals were segregated in small containers so that the movements of the emerging cercariae could be studied before microscopical studies were made. Later, cysts were recovered for study from the inner walls of these containers and from the snails themselves since they often serve as the host of the encysted forms as well, particularly for the echinostome cercariae.

Incidence of emergence could be studied too, and has been mentioned in the descriptions of some species. Parasitized snails frequently die in the laboratory, although, in some cases, it has been possible to keep severely parasitized hosts for long periods.

Cercariae were fixed with warm Gilson's fluid, saturated corrosive sublimate fixing fluid, and corrosive acetic. Sections of the liver, including sporocysts or rediae, were also fixed and in all cases preserved in 75% alcohol. Entire mounts of the cercariae, sporocysts, and rediae were made for additional study and later reference, after staining with Delafield's hematoxylin, Ehrlich's acid hematoxylin, Mayer's paracarmine, alum cochineal, and Mallory's phospho-tungstic hematoxylin.

In addition to the methods mentioned above, intra-vitam staining was used in these studies. The use of neutral red for staining certain glands and organs in the living animal proved to be very valuable, particularly for distinguishing the number of penetration glands and the slender, undeveloped ceca of the digestive system, both important points in identification. Weak solutions of methylene blue, introduced under the coverslip, aided in locating spines of the tail and body, and the collar spines of echinostome cercariae.

III. DISCUSSION OF INFECTION RECORDS

An examination of the data on molluscan infection with the cercariae discussed in this survey brings out a number of interesting features of the work. As previously mentioned, the reporting of many molluscan hosts for the same species of cercaria in the same locality has been questioned. However, Cort (1918) gave several striking examples of the lack of specificity in the choice of intermediate hosts, notably the human schistosome cercariae, *C. douthitti* Cort 1914 and *C. douglasi* Cort 1917. He submitted data to support this contention and said: "The data given above seems to clearly indicate that the forked-tailed cercariae readily adapt themselves to new molluscan intermediate hosts."

Many species have now been reported from a wide variety of hosts. From my own records I can say with certainty that *C. acanthocoela* has been found in *Physa gyrina hildrethiana* and *Helisoma trivolvis;* that *C. mesotyphla* occurs in *Physa gyrina hildrethiana, P. halei,* and *P. gyrina;* that *C. pteractinota* infests both *P. gyrina* and *H. trivolvis;* and that *C. trivolvis* Cort 1914 was found in both *H. trivolvis* and *P. gyrina.* In fact the very existence of many forms depends upon their cosmopolitan adjustment to various hosts in different localities. This has been proved by distributional and experimental studies.

Miller and Northup (1926) concluded that there is a semi-annual rise and fall in the larval trematode infestation of *Nassa obsoleta.* They believed this was due to the migration of the definitive hosts and the degree of their infestation, as well as the life span of Nassa and the

effect of parasitism upon it. While my collections were not regular enough to base such conclusions on them, there is some evidence in Table I to show the effect of the long severe summer drouth of 1931 on the larval trematode fauna of gastropods. The instability of this fauna in a particular body of water is also apparent. No doubt many of the holostome cercariae, as well as others, reach local bodies of water through the infected excrement of migrant or summer-resident birds. A certain species of cercaria may be found only once in a given locality, even though collections are continued over a period of several years. But even though many of the species studied are isolated in particular bodies of water, several forms, such as *C. pteractinota, C. trivolvis,* and *C. mesotyphla* appear to be distributed generally over the area represented by the collections (see Table II).

The data offered by former workers to show the percentage of infection which they found for larval trematodes were a compilation showing the total number of infected snails, that is, both those with undeveloped cercariae and those with emerging cercariae. My data represent an attempt to determine the periods when emergence is normally at its height. Therefore, infections showing only completely developed cercariae are included in the following tables and are represented in the computations of Table IV.

Cort (1922) gave some idea of the enormous number of cercariae that may emerge from a single snail host. He also showed the definite relation between the number of sporocysts present in the snail and its output of cercariae. Temperature has been shown by various workers to be an important regulator of the emergence of cercariae from their hosts. Studies of infected snails after they have been kept in the laboratory for a long period without feeding, indicate that the number of escaping cercariae is greatly reduced by starving the host. In these cases the sporocysts have always contained relatively few cercariae, and in many cases I have noticed dead cercariae and disintegrating germ balls within the cavity of the sporocyst or redia.

An examination of Table IV shows that *Cercaria meniscadena* is the commonest form found in the Urbana area, since over 10% of the *Pleurocera acuta* collected were infected with emerging cercariae. In all, emerging cercariae from about one hundred snails were studied. These infected snails represent about 2.98% of the total number collected from all localities. A few snails were collected at Baton Rouge, Louisiana, Sinking Creek and St. Charles, Missouri, and Leesburg, Florida. These localities have been clearly indicated in Tables I and II. All other collections were made in Illinois, chiefly in the vicinity of the University of Illinois at Urbana.

TABLE I.—COLLECTION RECORDS INCLUDED IN THIS STUDY

(Only completely developed cercariae are listed.)

Date	Place at Which Collected	Collections of Mollusks			Species of Cercariae described in this paper
		Scientific Name	Number Collected	Number Infected	
9/21/31	Oxbow, Urbana	*Physa gyrina hildrethiana*	32	0	
		Helisoma trivolvis	33	0	
9/22/31	Oxbow, Urbana	*P. gyrina hildrethiana*	36	0	
		H. trivolvis	10	0	
9/24/31	Oxbow, Muncie	*P. gyrina hildrethiana*	107	1	*C. mesotyphla* E. L. Miller 1935
9/26/31	Pond, Mahomet	*H. trivolvis*	18	0	
		P. gyrina hildrethiana	6	0	
9/29/31	Salt Fork River, Homer	*Goniobasis livescens*	27	0	
9/30/31	Caldwell's Lake, Seymour	*P. gyrina hildrethiana*	5	0	
10/2/31	Sangamon River, Mahomet	*Pleurocera acuta*	20	0	
10/5/31	Sangamon River, Mahomet	*P. acuta*	177	23	*C. meniscadena* E. L. Miller 1935
10/8/31	Twin Lakes, Paris	*Physa gyrina*	26	1	*C. pteractinota* E. L. Miller 1935
		H. trivolvis	5	0	

TABLE I.—COLLECTION RECORDS INCLUDED IN THIS STUDY (*Continued*)

(Only completely developed cercariae are listed.)

Date	Place at Which Collected	Collections of Mollusks			Species of Cercariae described in this paper
		Scientific Name	Number Collected	Number Infected	
10/8/31.....	Cole's Pond, Charleston	*Succinea ovalis*	2	1	*L. problematicum* Magath 1920
10/21/31.....	Oxbow, Urbana	*P. gyrina hildrethiana*	28	0	
		H. trivolvis	156	2	*C. hamata* Miller 1923
				1	*C. pteractinota* E. L. Miller 1935
10/22/31.....	Twin Lakes, Paris	*P. gyrina*	76	0	
	Cole's Pond, Charleston	*P. gyrina*	12	0	
		H. trivolvis	12	0	
10/23/31.....	Drainage Ditch, Urbana	*H. trivolvis*	12	1	*C. acanthocoela* E. L. Miller 1935
10/26/31.....	Camp Creek, Seymour	*P. gyrina hildrethiana*	74	1	*C. mesotyphla* E. L. Miller 1935
				8	*C. urbanensis* Cort 1914
		H. trivolvis	37	1	*C. pteractinota* E. L. Miller 1935
				1	*C. trivolvis* Cort 1914
				1	*C. pachycystata* E. L. Miller 1935

TABLE I.—COLLECTION RECORDS INCLUDED IN THIS STUDY (*Continued*)

(Only completely developed cercariae are listed.)

Date	Place at Which Collected	Collections of Mollusks			Species of Cercariae described in this paper
		Scientific Name	Number Collected	Number Infected	
10/27/31	Camp Creek, Seymour	*P. gyrina hildrethiana*	221	4	*C. urbanensis* Cort 1914
10/28/31	Leesburg, Florida	*Ampullaria depressa*	3	1	*C. cystonchnoides* E. L. Miller 1935
		Viviparus georgiana	175	3	*C. cyclica* nov. sp.
11/1/31	Sangamon River, Mahomet	*P. acuta*	7	0	
	Camp Creek, Seymour	*H. trivolvis*	30	1	*C. acanthocoela* E. L. Miller 1935
11/4/31	Sangamon River, Mahomet	*Actinonaias carinata*	2	1	*C. mitocerca* E. L. Miller 1935
11/10/31	Lake Decatur, Decatur	*P. gyrina hildrethiana*	512	2	*C. hamata* Miller 1923
11/18/31	Kaskaskia River, Sadorus	*P. gyrina hildrethiana*	39	0	
11/24/31	Oxbow, St. Joseph	*Musculium transversum*	28	2	*C. sphaerocerca* E. L. Miller 1935
12/8/31	Oxbow, St. Joseph	*P. gyrina hildrethiana*	12	0	

TABLE I.—COLLECTION RECORDS INCLUDED IN THIS STUDY (*Continued*)

(Only completely developed cercariae are listed.)

Date	Place at Which Collected	Collections of Mollusks			Species of Cercariae described in this paper
		Scientific Name	Number Collected	Number Infected	
12/28/31.....	Sangamon River, Mahomet	*Campeloma sp.*	18	0	
4/4/32.....	Camp Creek, Seymour	*P. gyrina hildrethiana*	65	1	*C. acanthocoela* E. L. Miller 1935
				1	*C. multicellulata* Miller 1923
				1	*C. steganocoela* E. L. Miller 1935
4/8/32.....	Cole's Stream, St. Charles, Missouri	*Physa halei*	126	0	
	Alhambra	*P. halei*	140	1	*C. mesotyphla* E. L. Miller 1935
4/10/32.....	Camp Creek, Seymour	*P. gyrina hildrethiana*	8	0	
4/15/32.....	Sinking Creek, Mo., Shannon County	*Goniobasis sp.*	61	0	
4/19/32.....	Oxbow, Urbana	*H. trivolvis*	12	0	
4/21/32.....	Pollywogs, St. Joseph	*P. gyrina*	52	0	
		H. trivolvis	18	1	*C. acanthocoela* E. L. Miller 1935

TABLE I.—COLLECTION RECORDS INCLUDED IN THIS STUDY (*Continued*)

(Only completely developed cercariae are listed.)

Date	Place at Which Collected	Collections of Mollusks			Species of Cercariae described in this paper
		Scientific Name	Number Collected	Number Infected	
4/26/32	Baton Rouge, Louisiana	*Helisoma lantum*	28	1	*C. tridena* nov. sp.
				2	*C. bessiae* Cort and Brooks 1928
				1	*C. furcalineata* nov. sp.
5/2/32	Stream, Muncie	*P. gyrina*	138	0	
5/5/32	East Lake Fork, Sadorus	*H. trivolvis*	58	0	
		P. gyrina hildrethiana	352	1	*C. mesotyphla* E. L. Miller 1935
				1	*C. steganocoela* E. L. Miller 1935
5/8/32	Sewage Ditch, Urbana	*P. gyrina hildrethiana*	7	1	*C. steganocoela* E. L. Miller 1935
		Fossaria obrussa	17	0	
	Pond No. 4, Urbana	*H. trivolvis*	12	0	
		P. gyrina	11	0	
		Lymnaea sp.	11	0	

TABLE I.—COLLECTION RECORDS INCLUDED IN THIS STUDY (*Continued*)

(Only completely developed cercariae are listed.)

Date	Place at Which Collected	Collections of Mollusks			Species of Cercariae described in this paper
		Scientific Name	Number Collected	Number Infected	
5/12/32.....	Salt Fork River, Homer	*G. livescens*	265	10	*C. cystorhysa* E. L. Miller 1935
5/29/32.....	Sangamon River, Mahomet	*P. gyrina*	2	1	*C. gigas* Faust 1918
6/8/32.....	Oxbow, St. Joseph	*P. gyrina*	11	1	*C. mesotyphla* E. L. Miller 1935
		H. trivolvis	10	1	*C. trivolvis* Cort 1914
6/12/32.....	Mud Slough, Henry	*H. trivolvis*	12	1	*C. pachycystata* E. L. Miller 1935
6/14/32.....	Oxbow, St. Joseph	*P. gyrina*	3	2	*C. mesotyphla* E. L. Miller 1935
		H. trivolvis	35	1	*C. trivolvis* Cort 1914
				2	*C. hamata* Miller 1923
					C. pteractinota E. L. Miller 1935

TABLE I.—COLLECTION RECORDS INCLUDED IN THIS STUDY (*Concluded*)

(Only completely developed cercariae are listed.)

Date	Place at Which Collected	Collections of Mollusks			Species of Cercariae described in this paper
		Scientific Name	Number Collected	Number Infected	
6/18/32.....	Baton Rouge, Louisiana	*H. lantum*	11	1	*C. tricystica* E. L. Miller 1935
6/19/32.....	Baton Rouge, Louisiana	*P. gyrina*	14	1	*C. pteractinota* E. L. Miller 1935
				1	*C. louisiana* E. L. Miller 1935
6/25/32.....	Oxbow, St. Joseph	*H. trivolvis*	90	1	*C. acanthocoela* E. L. Miller 1935
7/7/32.....	Pond, Rantoul	*P. gyrina*	12	3	*C. mesotyphla* E. L. Miller 1935
	Oxbow, St. Joseph	*H. trivolvis*	14	6	*C. trivolvis* Cort 1914
7/9/32.....	Oxbow, St. Joseph	*H. trivolvis*	26	2	*C. wardi* Miller 1923
				1	*C. trivolvis* Cort 1914
				1	*C. hamata* Miller 1923
				1	*C. acanthocoela* E. L. Miller 1935
		P. gyrina	5	1	*C. trivolvis* Cort 1914

TABLE II.—REGIONS OF SPECIFIC CERCARIAL INFESTATIONS

Locality	Molluscan Hosts	Cercariae
Alhambra	*Physa halei*	*C. mesotyphla*
Baton Rouge, Louisiana	*Helisoma lantum*	*C. tricystica* *C. tridena* *C. bessiae* *C. furcalineata*
	Physa gyrina	*C. pteractinota* *C. louisiana*
Caldwell's Lake, Seymour	*Physa gyrina hildrethiana*	None
Camp Creek, Seymour	*Physa gyrina hildrethiana*	*C. acanthocoela* *C. multicellulata* *C. steganocoela* *C. mesotyphla* *C. urbanensis*
	Helisoma trivolvis	*C. pteractinota* *C. trivolvis* *C. pachycystata* *C. acanthocoela*
Cole's Pond, Charleston	*Succinea ovalis*	*L. problematicum*
	Physa gyrina	None
	Helisoma trivolvis	None
Cole's Stream, St. Charles, Missouri	*Physa crandalli*	None
Drainage Ditch, Urbana	*Helisoma trivolvis*	*C. acanthocoela*
East Lake Fork, Sadorus	*Physa gyrina hildrethiana*	*C. mesotyphla* *C. steganocoela*
	Helisoma trivolvis	None
Kaskaskia River, Sadorus	*Physa gyrina hildrethiana*	None
Lake Decatur, Decatur	*Physa gyrina hildrethiana*	*C. hamata*
Leesburg, Florida	*Ampullaria depressa*	*C. cystonchnoides*
	Viviparus georgiana	*C. cyclica*
Mud Slough, Henry	*Helisoma trivolvis*	*C. pachycystata*
Oxbow, Muncie	*Physa gyrina hildrethiana*	*C. mesotyphla*

TABLE II.—REGIONS OF SPECIFIC CERCARIAL INFESTATIONS (*Concluded*)

Locality	Molluscan Hosts	Cercariae
Oxbow, St. Joseph	*Musculium transversum*	*C. sphaerocerca*
	Physa gyrina hildrethiana	None
	Physa gyrina	*C. trivolvis*
		C. mesotyphla
	Helisoma trivolvis	*C. trivolvis*
		C. hamata
		C. pteractinota
		C. acanthocoela
		C. wardi
Oxbow, Urbana	*Physa gyrina hildrethiana*	None
	Physa gyrina	None
	Helisoma trivolvis	*C. hamata*
		C. pteractinota
Pollywogs, St. Joseph	*Physa gyrina*	None
	Helisoma trivolvis	*C. acanthocoela*
Pond, Mahomet	*Helisoma trivolvis*	None
	Physa gyrina hildrethiana	None
Pond No. 4, Urbana	*Helisoma trivolvis*	None
	Physa gyrina	None
	Lymnaea sp.	None
Pond, Rantoul	*Physa gyrina*	*C. mesotyphla*
Salt Fork River, Homer	*Goniobasis livescens*	*C. cystorhysa*
Sangamon River, Mahomet	*Pleurocera acuta*	*C. meniscadena*
	Actinonaias carinata	*C. mitocerca*
	Campeloma sp.	None
	Physa gyrina	*C. gigas*
Sinking Creek, Missouri, Shannon County	*Goniobasis sp.*	None
Sewage Ditch, Urbana	*Fossaria obrussa*	None
	Physa gyrina hildrethiana	*C. steganocoela*
Stream, Muncie	*Physa gyrina*	None
Twin Lakes, Paris	*Physa gyrina*	*C. pteractinota*
	Helisoma trivolvis	None

TABLE III.—PERCENTAGE OF INFECTION OF EACH MOLLUSK HOST WITH EACH CERCARIA STUDIED

Cercaria	Molluscan Host	Number Collected	Number Infected	Percentage of Infection
C. acanthocoela	*Physa gyrina hildrethiana*	1492	1	0.07
C. acanthocoela	*Helisoma trivolvis*	600	5	0.83
C. bessiae	*Helisoma lantum*	39	2	5.13
C. cyclica	*Viviparus georgiana*	175	3	1.71
C. cystonchnoides	*Ampullaria depressa*	3	1	33.3
C. cystorhysa	*Goniobasis livescens*	291	10	3.44
C. furcalineata	*Helisoma lantum*	39	1	2.57
C. gigas	*Physa gyrina*	232	1	0.43
C. hamata	*Helisoma trivolvis*	600	3	0.50
C. hamata	*P. gyrina hildrethiana*	1492	2	0.13
C. louisiana	*Physa gyrina*	232	1	0.43
C. meniscadena	*Pleurocera acuta*	228	23	10.09
C. mesotyphla	*Physa gyrina hildrethiana*	1492	3	0.20
C. mesotyphla	*Physa halei*	266	1	0.38
C. mesotyphla	*Physa gyrina*	232	6	2.59
C. mitocerca	*Actinonaias carinata*	2	1	50.00
C. multicellulata	*Physa gyrina hildrethiana*	1492	1	0.07
L. problematicum	*Succinea ovalis*	2	1	50.00
C. pteractinota	*Physa gyrina*	232	2	0.86
C. pteractinota	*Helisoma trivolvis*	600	3	0.50
C. sphaerocerca	*Musculium transversum*	28	2	7.14
C. steganocoela	*Physa gyrina hildrethiana*	1492	3	0.20
C. pachycystata	*Helisoma trivolvis*	600	2	0.33
C. tricystica	*Helisoma lantum*	39	1	2.57
C. tridena	*Helisoma lantum*	39	1	2.57
C. trivolvis	*Helisoma trivolvis*	600	10	1.67
C. trivolvis	*Physa gyrina*	232	1	0.43
C. urbanensis	*Physa gyrina hildrethiana*	1492	12	0.83
C. wardi	*Helisoma trivolvis*	600	2	0.33

TABLE IV.—PERCENTAGE OF CERCARIAL INFECTION FOR EACH SPECIES OF SNAIL HOST

Snail Host	Number Collected	Number Infected	Percentage
Physa gyrina hildrethiana	1492	22	1.47
Helisoma trivolvis	600	23	3.83
Helisoma lantum	39	5	13.00
Viviparus georgiana	175	3	1.14
Ampullaria depressa	3	1	33.33
Goniobasis livescens	291	10	3.44
Pleurocera acuta	228	23	10.08
Physa gyrina	232	11	4.73
Physa halei	266	1	.38
Total	3326	99	Average 2.98

IV. DISCUSSION AND KEY TO THE ILLINOIS CERCARIAE

Cort (1914, 1915) was the first worker to describe cercariae from Illinois, and he also described these forms more completely than had been done for any North American larval forms up to that time.

Since then other workers, notably Faust (1918a, 1918b), Miller (1923, 1926a), Beaver (1929), and Horsfall (1930), have published detailed descriptions of one or more Illinois forms. Other references (Faust, 1919; Hopkins, 1933; and Horsfall, 1933) have been made to Illinois larval forms but so far as I am able to determine no other cercariae have been described in enough detail so that they may be included in the following key to the Illinois species.

The present paper includes descriptions of two Gorgoderine Cercariae, six xiphidiocercariae and five furcocercous cercaria, all from Illinois. In addition, a cercariaeum, *Leucochloridium problematicum* Magath 1920, formerly reported from Iowa, has been found in Illinois. This brings the number of described forms from Illinois up to thirty-eight.

C. urbanensis has been found by the author in a new locality, namely Seymour, also *C. trivolvis* at Seymour and St. Joseph. In addition to infecting *Helisoma trivolvis, C. trivolvis* was also found in *Physa gyrina. L. problematicum* was found at Charleston in an additional species of Succinea, namely *S. ovalis.* Other new localities are Mahomet for *C. gigas,* Seymour for *C. multicellulata,* St. Joseph and Decatur for *C. hamata,* and St. Joseph for *C. wardi.*

A list of the Illinois forms, together with the localities and hosts from which they were reported by various authors, includes the following cercariae.

Monostome Cercariae

1. *C. urbanensis* Cort 1914; from Urbana and Seymour; in *Physa gyrina.*
2. *C. robusta* Faust 1918; from DeKalb; in *P. gyrina.*
3. *C. aurita* Faust 1918; from Homer; in *Goniobasis pulchella.*
4. *C. spatula* Faust 1919; from Urbana; in *P. gyrina.*
5. *C. infracaudata* Horsfall 1930; from Homer; in *Goniobasis livescens.*

Amphistome Cercariae

1. *C. diastropha* Cort 1914; from Chicago; in *Helisoma trivolvis.*
2. Cercaria of *Allassostoma parvum* according to Beaver, 1929.
   Synonyms according to Beaver:
   C. inhabilis Cort 1914; from Urbana; in *H. trivolvis.*
   C. convoluta Faust 1919; from Urbana; in *H. trivolvis.*

ECHINOSTOME CERCARIAE

1. *C. trivolvis* Cort 1914; from Urbana, DeKalb, Seymour, and St. Joseph; in *H. trivolvis* and *P. gyrina.*
2. *C. reflexae* Cort 1914; from Chicago; in *Lymnaea reflexa.*
3. *C. chisolenata* Faust 1918; from Mt. Morris; in *P. gyrina.*
4. *C. acanthostoma* Faust 1918; from Urbana; in *H. trivolvis* and *P. gyrina.*
5. *C. complexa* Faust 1919; from Urbana; in *H. trivolvis.*

GYMNOCEPHALOUS CERCARIAE

1. *C. megalura* Cort 1914; from Mahomet; in *Pleurocera elevatum.*

CYSTOCERCOUS CERCARIAE

1. *C. macrostoma* Faust 1918; from Urbana, Homer, and Evanston; in *G. livescens.*

GORGODERINAE CERCARIAE

1. *C. sphaerocerca* E. L. Miller 1935; from St. Joseph; in *Musculium transversum.*
2. *C. mitocerca* E. L. Miller 1935; from Mahomet; in *Actinonaias carinata.*

CERCARIAEA

1. *Leucochloridium problematicum* Magath 1920; from Charleston; in *Succinea ovalis.*

FURCOCERCOUS CERCARIAE

1. *C. douthitti* Cort 1914; from Chicago; in *Lymnaea reflexa.*
2. *C. gigas* Faust 1918; from DeKalb, Mt. Morris, Urbana, and Mahomet; in *H. trivolvis* and *P. gyrina.*
3. *C. minima* Faust 1918; from DeKalb; in *P. gyrina.*
4. *C. robusticauda* Faust 1919; from Urbana; in *P. gyrina.*
5. *C. rhabdocaeca* Faust 1919; from Urbana; in *H. trivolvis.*
6. *C. multicellulata* Miller 1923; from Urbana and Seymour; in *P. gyrina.*
7. *C. hamata* Miller 1923; from Urbana, St. Joseph, and Decatur; in *H. trivolvis.*
8. *C. wardi* Miller 1923; from Urbana and St. Joseph; in *H. trivolvis.*
9. *C. pteractinota* E. L. Miller 1935; from Paris; in *P. gyrina.*

XIPHIDIOCERCARIAE

1. *C. hemilophura* Cort 1914; from Rockford; in *P. gyrina.*
2. *C. isocotylea* Cort 1914; from Urbana and DeKalb; in *H. trivolis.*
3. *C. polyadena* Cort 1914; from Chicago; in *Lymnaea reflexa.*
4. *C. stilifera* Faust 1918; from Mt. Morris; in *P. gyrina.*
5. *C. trifurcata* Faust 1919; from Urbana; in *P. gyrina.*
6. *C. candelabra* Faust 1919; from Urbana; in *H. trivolvis.*
7. *C. mesotyphla* E. L. Miller 1935; from Muncie, Seymour, Sadorus, Alhambra, St. Joseph, and Rantoul; in *P. gyrina, P. gyrina hildrethiana,* and *P. halei.*
8. *C. cystorhysa* E. L. Miller 1935; from Homer; in *Goniobasis livescens.*
9. *C. meniscadena* E. L. Miller 1935; from Mahomet; in *Pleurocera acuta.*
10. *C. acanthocoela* E. L. Miller 1935; from Urbana, St. Joseph, and Seymour; in *H. trivolvis* and *P. gyrina hildrethiana.*
11. *C. steganocoela* E. L. Miller 1935; from Seymour, Sadorus, and Urbana; in *P. gyrina hildrethiana.*
12. *C. pachycystata* E. L. Miller 1935; from Seymour and Henry; in *H. trivolvis.*

The above forms have been arranged in the form of a key for convenience in identification.

Key to the Illinois Cercariae

1 (52) (71) Cercariae with tail which is not forked..... 2
2 (11) Only one sucker and that at anterior end—Monostome Cercariae..... 3
3 (4) Only two pigmented eye-spots—Binoculate Cercariae.....*C. aurita* Faust 1918.
4 (3) Three pigmented eye-spots—Trioculate Cercariae..... 5
5 (6) Body spines present.....*C. spatula* Faust 1919.
6 (5) Body spines not present..... 7
7 (8) Excretory system consisting of only a bladder and two large collecting tubules filled with granules.....*C. urbanensis* Cort 1914.
8 (7) Excretory system with accessory capillaries and flame cells..... 9
9 (10) Caudal excretory tubule unbranched, except at terminal fork; bladder U-shaped.....*C. infracaudata* Horsfall 1930.
10 (9) Caudal excretory tubule with many branches; bladder spherical.....*C. robusta* Faust 1919.
11 (2) Body possesses two suckers.....12
12 (15) Second sucker ventral and at posterior end of body—Amphistome Cercariae.....13
13 (14) Body unpigmented except for narrow area around eyes.....*C. diastropha* Cort 1914.
14 (13) Anterior one-third to one-half of body heavily pigmented.....Cercaria of *Allassostoma parvum* Cort 1914.
15 (12) Second sucker ventral but not at posterior end of body.....16
16 (21) Body possesses long heavy tail not used in swimming.....17
17 (18) Tail has invaginated distal end; not swollen at base—Gymnocephalous Cercariae.....*C. megalura* Cort 1914.
18 (17) With heavy tail swollen at proximal end, into which the body may be withdrawn—Gorgoderine Cercariae.....19
19 (20) Distal portion of tail long and filiform; no stylet.....*C. sphaerocerca* E. L. Miller 1935.
20 (19) Distal portion of tail not filiform; stylet present.....*C. mitocerca* E. L. Miller 1935.
21 (16) Tail slender and used in swimming.....22
22 (43) Stylet present.....23
23 (27) Tail with fin-fold—Cercariae Ornatae.....24
24 (25) (26) Excretory bladder club-shaped.....*C. hemilophura* Cort 1914.
25 (24) (26) Excretory bladder small, crenate, with anterior end prolonged into two lateral collecting tubules.....*C. trifurcata* Faust 1919.
26 (24) (25) Excretory bladder with two vesicles separated by a very narrow constriction.....*C. mesotyphla* E. L. Miller 1935.
27 (23) Tail without fin-fold.....28
28 (31) One or two penetration glands on each side—Cercariae Microcotylae....29
29 (30) With characteristically wrinkled, rectangular bladder.....*C. cystorhysa* E. L. Miller 1935.
30 (29) With U-shaped bladder.....*C. meniscadena* E. L. Miller 1935.
31 (28) More than two penetration glands on each side—Cercariae Armatae.....32
32 (42) Elongated bladder consisting essentially of a posterior vesicle and two lateral ones.....33
33 (34) Many bluish, oil-like droplets throughout body; four penetration glands on each side.....*C. pachycystata* E. L. Miller 1935.
34 (33) Body without oil-like droplets.....35
35 (38) No trace of digestive ceca posterior to pharynx.....36
36 (37) Six to eight penetration glands on each side...*C. isocotylea* Cort 1915.
37 (36) Ten to twelve penetration glands on each side.*C. polyadena* Cort 1914.
38 (35) With complete digestive tract, including ceca.....39
39 (40) (41) Twelve penetration glands on each side...*C. stilifera* Faust 1918.

40 (39) (41) Nine penetration glands on each side.....*C. steganocoela* E. L. Miller 1935.
41 (39) 40) Seven to eight penetration glands on each side.....*C. acanthocoela* E. L. Miller 1935.
42 (32) Bladder composed of anterior and posterior vesicle with medium constriction.....*C. candelabra* Faust 1919.
43 (22) Stylet absent; collar spines developed or absent—Echinostome Cercariae.....44
44 (49) Swollen excretory crura filled with crystals.....45
45 (46) Tail with fin-fold.....*C. trivolvis* Cort 1914.
46 (45) Tail without fin-fold.....47
47 (48) Collar of 40 spines.....*C. chisolenata* Faust 1918.
48 (47) Collar of 38 spines.....*C. complexa* Faust 1919.
49 (44) Excretory crura without crystals.....50
50 (51) Tail with fin-fold; no collar spines.....*C. reflexae* Cort 1914.
51 (50) Tail without fin-fold; collar spines present..*C. acanthostoma* Faust 1918.
52 (1) (71) Cercariae with forked tail.....53
53 (54) Large basal tail stem into which body can be withdrawn—Cystocercous Cercariae.....*C. macrostoma* Faust 1918.
54 (53) Body cannot be withdrawn into tail stem—Furcocercous Cercariae.....55
55 (60) With no ventral sucker.....56
56 (57) With two small pigmented eye-spots.....*C. multicellulata* Miller 1923.
57 (56) Without eye-spots.....58
58 (59) Oral sucker pyriform.....*C. rhabdocaeca* Faust 1919.
59 (58) Oral sucker oval in shape.....*C. hamata* Miller 1923.
60 (55) With ventral sucker.....61
61 (62) Without eye-spots.....*C. robusticauda* Faust 1919.
62 (61) With two pigmented eye-spots.....63
63 (64) Furcae longer than one-half the stem length....*C. minima* Faust 1918.
64 (63) Furcae shorter than one-half the stem length.....65
65 (66) A posterior mucin gland present.....*C. wardi* Miller 1923.
66 (65) No posterior mucin gland present.....67
67 (68) Four penetration glands on each side of body...*C. douthitti* Cort 1914.
68 (67) A great many penetration glands filling the entire region posterior to the eye-spots.....69
69 (70) Furcal fin-folds closely fluted; without furcal rays.....*C. gigas* Faust 1918.
70 (69) Furcal fin-folds braced with radial furcal rays.....*C. pteractinota* E. L. Miller 1935.
71 (1) (52) Tailless larvae—Cercariaea.....*Leucochloridium problematicum* Magath 1920.

V. CYSTOCERCOUS CERCARIAE OF LÜHE

For many years the term Cystocercous was used to designate a miscellaneous group of cercariae, each of which is able to draw its body within the tail appendage where it encysts or remains unencysted. The earliest form to be described for this group is *Cercaria macrocerca* Filippi 1854. All subsequently added members of the group also possessed very large tails and the name Macrocercous was naturally applied to such members. It was found some years ago when their life histories began to be worked out that this grouping was very artificial, and at present three distinct groups should be recognized. Various workers have

spoken of them as the Cystophorous Cercariae, the Cystocercous Cercariae, and the Macrocercous or Gorgoderine Cercariae. I shall consider them in the above order.

Cystophorous Cercariae

History and Definition

Wagener described the first cystophorous cercaria to be reported in 1866, and called it *Cercaria cystophora.* He found it in *Planorbis marginatus.* Sonsino (1892) described *C. capsularis* from *Cleopatra bulmoides* and later Looss (1896) said that it belonged to this group. Pelseneer (1906) reported two marine species of the group, namely *C. appendiculata* from *Natica alderi* and *C. vaullegeardii* from *Trochus cinerarius.*

When Lühe (1909) listed *C. cystophora* in his key to the Cystocercous Cercariae he said about it: "In die Kammer ist ausser dem Körper des späteren Distomums auch das seitlich abgeknickte Schwanzende Zurückziehbar. Entwicklung in Redien in Planorbis."

Sinitsin (1911) defined the group of Cystophorous Cercariae as: "Cercariae which are characterized by possessing a vesicular tail with various appendages upon it." He also added two new marine species.

Cort and Nichols (1920) gave a more detailed discussion of the Cystophorous Cercariae when they added a new species, *C. californiensis,* to the group. They assigned the following characteristics to the group:

1. All cystophorous cercariae except *C. vaullegeardii* develop in rediae.
2. Mother sporocysts where rediae develop have been described for *C. sagittarius* and *C. cystophora,* but none have been found where rediae contain rediae.
3. All species lack larval structures for penetration and encystment; stylet, cystogenous, and cephalic glands absent.
4. Each species has a tail with a central vesicle into which the body can be withdrawn.

Sewell (1922) refers four previously described cystophorous cercariae to his Appendiculata group, along with a new species, *Cercaria indicae* XXXV. His definition of the group can apply to all cystophorous cercariae but he does not explain why he has included only five of the ten forms known at that time in his new group. His definition follows:

(1) The distome body is somewhat elongate in shape and is colorless and transparent; the two suckers are of equal size.
(2) The mouth leads back to a pharynx which is followed by a triclad gut.
(3) The excretory bladder is elongate, reaching forward nearly to the acetabular margin.
(4) The tail is complex and consists of two parts, a distal, flattened or cylindrical process, and a proximal, rounded or oval, and much swollen portion that forms a cyst containing a long slender filament.
(5) Development occurs usually in rediae which in turn arise from sporocysts. The redia has a well-marked pharynx and gut, but is devoid of locomotor processes.

C. vaullegeardii and *C. capsularis* differ from the other members of Sewell's Appendiculata group in that they develop in sporocysts instead of in rediae as do the other species.

The following cystophorous cercariae have been described:

1. *Cercaria cystophora* Wagener 1866
2. *C. capsularis* Sonsino 1892
3. *C. appendiculata* Pelseneer 1906
4. *C. vaullegeardii* Pelseneer 1906
5. *C. sagittarius* Sinitsin 1911
6. *C. laqueator* Sinitsin 1911
7. *C. yoshidae* Yoshida 1917
8. *C. californiensis* Cort & Nichols 1920
9. *C. syringicauda* Faust 1922
10. *C. indicae* xxxv Sewell 1922
11. *C. calliostomae* Dollfus 1923
12. *C. invaginata* Faust 1924
13. *C. macrocercoides* Faust 1926 (*C. macrura* Faust 1921 preoccupied)
14. *C. biflagellata* Faust 1926
15. *C. projecta* Willey 1930

Cystocercous Cercariae

History and Definition

Braun (1891) first described and named one of these anchor-tailed cercariae and gave it the name of *Cercaria mirabilis.* Faust (1918c) added two new species, and described the group as follows:

> Aside from their anchor tail the species of this group possess other characters in common which demonstrate their close relationship. Among these are the crowded ceca with granular contents, the long median Y-shaped excretory bladder, the presence of the ovary and pair of testes close behind the acetabulum, and the swollen cirrus pouch anterior to the acetabulum. . . . In general, the cercariae develop as the parthenogenetic offspring of sporocysts. They are found in the respiratory or digestive organs of snails.

Sewell (1922) listed six of the eight forms belonging to this group that had been described up to that time in his new Mirabilis group. This Mirabilis group, which included only these six cercariae, he described as follows:

(1) Development probably occurs in sporocysts; but the parthenitae have only been recorded in three forms.

(2) The tail is extremely large and wide, and at its anterior end forms a cavity into which the distome may be partially or completely withdrawn, except in the case of *C. fusca,* in which it is connected to the body by a short fold.

(3) A pair of suckers are present.

(4) A well-developed pharynx appears to be present, and the alimentary canal consists of a very short oesophagus which almost at once divides into long wide intestinal caeca reaching back to the posterior end.

(5) The excretory vesicle is elongate and is continued forwards as a median tube to the acetabular region, where it divides into two lateral branches.

The list of described cystocercous forms consists of the following:

1. *Cercaria mirabilis* Braun 1891
2. *C. wrighti* Ward 1916
3. *C. anchoroides* Ward 1916
4. *C. macrostoma* Faust 1918
5. *C. brookoveri* Faust 1918
6. *C. fusca* Pratt 1919
7. *C. pekinensis* Faust 1921
8. *C. stephanocauda* Faust 1921
9. *C. splendens* Szidat 1932
10. *C. melanophora* Smith 1932
11. *C. hodgesiana* Smith 1932

Gorgoderine Cercariae

History and Definition

The first cercaria described which belongs in this group is *Cercaria macrocerca* Filippi 1855. Later Wagener (1857) and Thiry (1860) reported this species, but Sinitsin (1905) demonstrated that their reports represented distinct species. Others worked on the life cycles of these forms, but much of the work was not experimentally conclusive.

Lühe (1909) and Sinitsin (1905) agree in calling the *C. macrocerca* of Thiry (1860) a new species. Sinitsin described it (1905) and named it *Cercaria gorgoderae pagenstecheri.* Sinitsin also demonstrated that the *C. macrocerca* of Wagener was a distinct species and named it *Cercaria gorgoderae loossi.* In 1905 Sinitsin described *Cercaria gorgoderae varsoviensis.* The life history discussions which Sinitsin submitted lack experimental evidence.

Kowalewski (1904) described *Cercaria gorgoderae cygnoidis* and Lühe agrees that this is the larva of *Gorgodera cygnoides.*

The following list includes all gorgoderine cercariae that have been described up to the present time.

1. *Cercaria macrocerca* Filippi 1854
2. *Cercaria gorgoderae cygnoidis* Kowalewski 1904
3. *Cercaria gorgoderae loossi* Sinitsin 1905
4. *Cercaria gorgoderae pagenstecheri* Sinitsin 1905
5. *Cercaria gorgoderae varsoviensis* Sinitsin 1905
6. *Cercaria sphaerocerca* E. L. Miller 1935
7. *Cercaria mitocerca* E. L. Miller 1935

When Lühe (1909) separated these forms from the cystocercous cercariae he described them as follows: "Schwanz ziemlich drehrund und nicht gabelig. Bohrstachel vorhanden. Sporocysten in Sphaerium. (Macrocerke Cercarien von Gorgoderien)."

Sewell divided this group into two divisions according to the relation of the individuals to the adult genera Gorgodera and Gorgoderina, but since experimental evidence for such a classification is lacking, I am omitting this subdivision.

During my study of cercariae of the Urbana region, I examined specimens of *Musculium transversa,* taken from the Salt Fork Oxbow just north of St. Joseph, Illinois, on November 24, 1931, and again on February 20, 1932, and found them to be infected with a gorgoderine cercaria. The individuals were found within the gill tissue of the Musculium, lying between the gill filaments. After considerable study I found it to be a new species of cercaria which very likely is a larva of one of the Gorgoderinae.

Cercaria sphaerocerca E. L. Miller 1935

(Figs. 1-9)

The distorted appearance of the body and the awkward shape and great size of the tail give to this cercaria a most unusual appearance which is quite distinctive from all other cercariae which I have either studied or noted. The tail is noticeably divided into two distinct regions, a narrow posterior region, greatly elongated, and a swollen or inflated anterior region resembling that of the other gorgoderine cercariae, and several times larger than the body of this cercaria (Fig. 4). At the proximal end of the tail is a bell- or funnel-shaped structure with thickened sides and a central core which serves as an attachment for the body of the cercaria. Just distal to this structure is a constricted, neck-like portion which separates the bell-shaped cyst cavity from the large tail globe. The body is elongate and narrow (Fig. 1), pointed at the posterior end when well extended, and rounded when contracted. The anterior end of the body is narrow but broadly rounded.

The body of this cercaria breaks loose from its tail easily and will do this readily when the cover-slip is pressed, or even because of its own movements in the tap water. I find that the cercariae have broken loose from their tails and are encysted inside the sporocysts after the dead tissues of the Musculium have been kept in tap water for about twenty-eight hours. However, they were found also encysted within the cyst cavity or expanded chamber at the proximal end of the tail (Fig. 3), which is quite probably their normal method of procedure. They twist about freely inside the cyst wall, this wall being thin, transparent, pliable and tough, so that it can be pushed out of its normal shape easily. A number of cysts were found in the containers but whether they were cysts of cercariae which had escaped from broken sporocysts, or were formed by cercariae which escaped normally from the sporocysts, is a point which was not determined.

Annular wrinkles extend around the body. Upon examination under high power these wrinkles appear to be horizontal rows of tiny swollen areas which are papillae. These papillae are less distinct on preserved cercariae. Projections are also located on the dorsal lip of the oral sucker. The body is an elongate oval in outline and the ventral sucker is a little posterior to the middle of the body. The posterior portion of the body proper is flattened and appears almost fan-shaped at times.

A small stylet is present, dorsal to the cavity of the oral sucker, but it is somewhat different from that described by earlier workers for other members of this group, as it lacks the lateral points along a ventral sharp blade as well as other structures so well illustrated by Sinitsin (1905),

and Lühe (1909) (Fig. 6). It is connected posteriorly by a group of from six to eight stylet glands on either side of the body just anterior to the acetabulum. These glands connect to a main duct which is bipartite at least in the anterior part of its course.

In the region of the body, posterior to the acetabulum and along either side of the elongated excretory bladder, is located a number of elongate glands in a rather regular group like those pictured for *Cercaria gorgoderae pagenstecheri* by Sinitsin (1905), but not in as regular a formation as those of *Cercaria gorgoderae loossi.* When, however, the bladder becomes deflated the regular character of these cells is more likely to be obscured.

The acetabulum is larger than the oral sucker and is posterior to the middle of the body, varying in position from a point just posterior to the center, to the anterior edge of the posterior one-third of the body, depending on the state of contraction since the posterior region of the body in particular is capable of contracting to an astonishing extent. In side view this sucker appears as a cup-shaped structure, attached by its base only to the body of the worm (Fig. 5). No pharynx or prepharynx is present; the esophagus extends posteriorly to a point about two-thirds of the distance from the oral sucker to the acetabulum, before it divides to form the intestinal crura. These crura reach a point slightly posterior to the halfway mark between the acetabulum and the posterior end of the body.

The excretory bladder is a long expulsion canal in this form, reaching from the posterior dorsal excretory pore to a point a short distance posterior to the acetabulum. In side view this bladder is a typical club-shaped structure with its enlarged end forward. Its shape is constantly changing but usually both an anterior and a posterior bulb are evident (Fig. 8). Two main collecting tubules divide into two branches just posterior to the anterior limits of their courses. The anterior branch redivides just posterior to the oral sucker. The posterior branch extends posteriad to a point slightly behind the acetabulum where it divides into two branches, the posterior one of which redivides immediately lateral to the excretory bladder. Finer branches and flame cells are present but their exact location has not been determined.

The following measurements were made while the living worm was subjected to rather strong pressure of the cover-slip, and during a state of contraction, in most cases. When the body is only partially extended it measures 0.576 mm. in length and 0.144 mm. at its greatest width, which is through the region of the acetabulum. The suckers were also measured when the worm was slightly extended and subjected to strong

pressure. The oral sucker is 85 μ long and 78 μ wide, while the acetabulum is 0.104 mm. in longitudinal diameter and 0.111 mm. in transverse diameter.

In measuring the tail greater pressure was necessary. The constricted region is 0.616 mm. long and the swollen portion, or globe, is only 0.392 mm. in length by 0.252 mm. in width. Because the greatest width was taken, it was necessary to measure the area just posterior to the center of the swollen part. The bell-like structure in which the cercaria was often found encysted, was measured after the cercaria had broken loose. It is 56 μ in length and 84 μ in width when it is contracted. The total length of the entire cercaria is about 1.64 mm.

The large tail is sluggish in its movements but after becoming detached in the water of the container sometimes remains active longer than the body. No definite bodies are discernible in this globe but it is composed of large, clear, irregular-shaped divisions (Fig. 2), which are easily seen when the worm is observed under high power of the microscope. These are similar to the divisions described by Sinitsin (1905) for *C. gorgoderae varsoviensis*. Rounded nuclear bodies are also located throughout this globe. Smaller angular bodies as well as larger rounded bodies are present but the triangular ones are more common in the posterior portion of the globe (Fig. 7).

In the region between the swollen and constricted portion of the tail, is a small group of tiny glands, which has also been noted in other closely related forms. There are smaller groups in other portions of the tail, with the exception of the central core. The narrow part of the tail, when at rest, possesses peculiar lateral folds which are always located in the same regions of the tail, two groups being on either side of the tail at the base of the constricted portion and two similar groups near the anterior edge of the posterior one-third of this part. It is possible that the muscle fibers of these regions function to produce the swaying, back-and-forth movement, mentioned by Lühe (1909) for similar forms.

This cercaria matures in an elongated irregular sac-like sporocyst which tapers at the end where it is attached to the gill tissue of the host and where there is a prominent knob projecting from the body, although this structure is not always present (Fig. 9). Only brief mention has been given to the sporocyst in descriptions of the few known closely related cercariae. Perhaps one reason for this is that the end opposite the knobbed end is filled with pigment which makes observation difficult. In fact the older sporocysts are not transparent enough to enable one to see the cercariae within, without rupturing the wall of the sporocyst. The young sporocyst extends and contracts in a sluggish manner, but is still as active as some of the cercariae. It is more transparent than those more advanced in age and the germ balls can be seen in

movement quite easily, as they are pushed from side to side during the movements of the sporocyst. The body wall is composed of unusually large cells and becomes thickened at each end of the sporocyst.

When the sporocyst is pressed the cercariae come out of it, and the body of the cercaria, which has been folded at the side of the swollen portion of the tail, when it was in the sporocyst, straightens. Many of the sporocysts contain only one cercaria; perhaps the long period of confinement of the host in the laboratory may have brought about this condition. This again, as has been formerly intimated, might indicate that infection of the molluscan host terminates of its own accord.

Encysted forms were found inside the bell of the tail of individuals in the container. When subjected to pressure of the cover-slip the encysted individual was forced through the opening at the tip of the bell. These recently encysted individuals conform with the description of the cercariae, in their appearance and measurements. Some cercariae have also been found broken loose from their tails and encysted inside the sporocysts that had been freed from the gills of the Musculium and left in water over night. Twenty-eight hours after encystment they were still active.

Cercaria mitocerca E. L. Miller 1935

(Figs. 10-15)

The material which furnished the basis for this study was taken from the liver tissue of *Actinonaias carinata* collected in the Sangamon River near Mahomet, Illinois, on Nov. 4, 1932. Very few cercariae from the Unionidae have been reported in North America. This is particularly striking when one considers the abundance of these mollusks in almost all parts of the United States. Altogether about twenty species of these Acephala from various parts of the world have been listed as harboring larval trematodes. From North America, Leidy (1858) reported *Cercaria duplicata* (Von Baer 1827), a rhopalocercous cercaria, and gave as its hosts *Anodonta fluviatilis* and *A. lacustris.*

This cercaria resembles the other gorgoderine cercariae very much, but differs in that it has no stylet. There is no other cercarial group whose members resemble more closely this species, and since it is very similar to these species with the exception which I have noted above, I am including it here.

This cercaria resembles *C. sphaerocerca,* in that it possesses a long tail greatly swollen into a large body at its proximal end, and a narrow distal portion. This posterior portion is very narrow and elongated, being almost threadlike in its appearance (Fig. 12).

The body is large, and elongated when extended, but when mediumly contracted the posterior end appears as a wide flare (Fig. 11) extending

laterally from the sides of the body just posterior to the acetabulum, and much more compressed dorso-ventrally than the rest of the body. The edges of this portion of the body, when the worm contracts, resemble the lobate edge of a contracted turbellarian. The posterior end is quadrate with a constriction in the region of the excretory pore. Lateral constrictions occur on either side of the body just anterior to the ventral sucker (Fig. 10). This feature is evident in nearly all of the cercariae described by Sinitsin (1905) belonging to this group. The surface of the body is broken by several rather prominent papillae which are more common on the anterior end. They extend posteriad along the sides to slightly beyond the posterior limits of the oral sucker.

The size of the body varies greatly according to the state of contraction. When well extended it often is 1.12 mm. in length and 0.269 mm. in greatest width, which in this form is in the region just posterior to the acetabulum, due to the lateral flare already mentioned. When contracted the body is only 0.728 mm. by 0.448 mm., and when only mediumly extended it is 0.952 mm. by 0.336 mm. The portion immediately posterior to the acetabulum often flares outward, out of all proportion to the rest of the body, measuring sometimes as much as 0.504 mm. in width.

The oral sucker is terminal and the mouth opening is ventral. From side view the acetabulum is seen projecting ventrally. The oral sucker is slightly longer than it is wide; it is 0.14 mm. by 0.129 mm. when the worm is only slightly contracted. The acetabulum is located near the middle of the body; it is smaller than the oral sucker and is spherical, being about 0.126 mm. in diameter. It is located about 0.28 mm. posterior to the oral sucker and 0.504 mm. from the posterior end of the body.

The oral sucker opens into an esophagus, no pharynx being present, and extends for approximately one-half the distance from the oral sucker to the acetabulum before dividing to form the two intestinal crura, which are relatively large and which extend to within 0.13 mm. of the posterior end of the body. However, this distance varies greatly with extension and contraction. The esophagus is about 0.104 mm. in length.

No stylet is present, but ducts can be seen running posteriorly from the sides of the oral sucker in a lateral position. The location and number of glands could not be determined in this form, due to the presence of many small cells in this region of the body.

Extending from the posterior end of the body to within a short distance of the acetabulum is the elongated excretory bladder or expulsion canal. When contracted the sides are irregular and the posterior end is swollen into a slight bulb. This bladder and the main collecting tubules resemble greatly those of *C. sphaerocerca*. It divides anteriorly to form the two main collecting tubules which, in the anterior region of the

body, turn posteriorly and run the entire length of the body again. They become indistinct in the maze of tubules, large and small, which ramify the body in all directions. Large flame cells are present in the body.

A mass of large spherical bodies fills the major part of the body posterior to the acetabulum, and when the body is well extended they seem to occupy a definite position and to resemble glands. They are circular but are not systematically arranged, as has been noted in other species (Fig. 11). Also in this area are located three bodies, two of which are lobed, and one unlobed, which I believe to be the reproductive glands. Since the left posterior one is five-lobed and the right anterior is four-lobed, I believe these bodies will give rise to the two testes, one of five parts and the other of four parts, in the adult. For this reason I believe the form may be the larval stage of an adult gorgoderine bladder fluke. The ovary is anterior to the left testis and immediately posterior to the acetabulum.

Like *C. sphaerocerca* this cercaria contains a long, tail-like structure, consisting of an anterior swollen area and a posterior constricted thread-like portion (Fig. 12). The thread contains a hollow core throughout its length, and there are scattered nuclei in both the globe and thread of the tail. The surface of the globe is covered with tiny fissures (Fig. 14), which have no definite arrangement but which connect and diverge in all possible directions.

At the proximal end of the globe is a spherical hollow structure having thickened walls (Fig. 13). The body is attached here, and, when it breaks loose, the opening snaps shut giving the appearance of a closed sphere. The globe measures about 0.448 mm. in length by 0.185 mm. in width, while the narrow portion has the great length of 2.128 mm. and a width near its base of only 22 μ. The width tapers only slightly toward the distal end of this thread.

The sporocysts which give rise to these cercariae are ovate, broadly-rounded sacs, some with contracted tips at the smaller end of the sac (Fig. 15). No independent movement was noted in these forms, even in the younger ones, but the cercariae could be seen within, moving about sluggishly. An average of the measurements of ten taken at random gives a length of 0.980 mm. and a width of 0.462 mm.

A few encysted individuals were found inside the sporocysts in the tissue of the mussel, which had been allowed to remain in water over night after it had been dissected, but there were no tails on these individuals. However, many of these forms remained alive in containers for 48 hours without encysting. Encysted individuals were enclosed by a spherical transparent wall, and they resembled the cercariae in all structural details.

VI. MONOSTOME CERCARIAE

History and Definition

Relatively few of the cercariae described can be placed in this group. Up to the time when Cort (1914) described *Cercaria urbanensis* from Illinois, only two reports of monostome cercariae were available from the literature from North America. Cort (1915) says that they have been known since 1817, but I know of no one of them of which the life history has been proved experimentally. Lühe (1909) described the group as: "Ohne Bauchsaugnapf, mit Augenflecken, Schwanz sinfach, lang, schlank, ohne Borstenbesatz. Entwicklung in Redien. Encystierung im Freien (ob bein allen Arten)."

None of these monostomes have been known to develop from sporocysts, but Looss (1896) states that in material of *C. imbricata* near Leipzig he had found rediae in which rediae were developing. A few forms belonging to this group have been described as having posterior locomotor projections on the rediae such as *C. imbricata* Looss 1893. Some of these rediae also bear peculiar constrictions in their bodies, for instance, *Cercaria urbanensis* Cort 1914 and *Cercaria* (*Glenocercaria*) *lucania* Leidy 1877.

Sewell (1922) used the term Monostome Cercariae in its broadest sense, to include "all these forms in which as the name implies, a ventral sucker or acetabulum is missing." Since then experimental life history work has been done, notably that by McCoy (1929a) on a lophocercous monostome cercaria, showing that the ventral sucker which has been absent in the cercaria, may develop in the metacercaria. Such discoveries have shown beyond doubt that Sewell's classification of these monostome cercariae is an unnatural one, since many of the forms which he includes in this group are in reality either xiphidiocercariae or furcocercous cercariae. He also divided all monostome cercariae into six subgroups and named them: Pleurolophocerca, Urbanensis, Ephemera, Lophocerca, Lophoides, and Ubiquita. An analysis of this classification shows groups Urbanensis and Ephemera to contain only those forms which had been considered true monostome cercariae up to that time. Sewell's Lophocerca and Lophoides groups contain only furcocercous cercariae while his Ubiquita group contains only stylet cercariae. The individuals of his Pleurolophocerca group differ from those of the Urbanensis and Ephemera groups in that the so-called oral sucker is really a penetrating organ or anterior organ similar to that of the furcocercous cercariae; there are no posterior locomotor pockets; the tail has cuticular fin-folds; and there is no trace of any esophagus or intestinal ceca.

Sewell's Urbanensis group corresponds in the main to the binoculate group of Faust (1917) and his Ephemera group to the trioculate group of Faust (1917). For the above reasons, I am limiting the monostome cercariae to Sewell's Urbanensis and Ephemera groups.

I find descriptions of the following species that belong to the Monostome Cercariae:

Binoculate Cercariae

1. *C. fulvoculata* Cawston 1911
2. *C. konadensis* Faust 1917
3. *C. aurita* Faust 1918
4. *C. hemispheroides* Faust 1924
5. *C. yenchingensis* Faust 1930

Trioculate Cercariae

1. *C. ephemera* Nitzch 1807
2. *C. hyalocauda* Haldemann 1842
3. *C. (Glenocercaria) lucania* Leidy 1877
4. *C. imbricata* Looss 1893
5. *C. monostomi* v. Linst. 1896
6. *C. zostera* Sinitsin 1911
7. *C. urbanensis* Cort 1914
8. *C. pellucida* Faust 1917
9. *C. robusta* Faust 1918
10. *C. spatula* Faust 1919
11. *C. indica* xi Sewell 1922
12. *C. plana* Faust 1922
13. *C. trabeculata* Faust 1924
14. *C. infracaudata* Horsfall 1930
15. *C. triophthalmia* Faust 1930
16. *C. lebouri* Stunkard 1932

Cercaria urbanensis Cort 1914

(Figs. 20-27)

Physa gyrina hildrethiana taken at Camp Creek near Seymour, Illinois, in October, 1931, was found to be infected in unusual numbers with a monostome cercaria, *C. urbanensis*. Study of this form revealed a number of interesting facts which have not been mentioned before.

Table I, which gives the infection records, will indicate that this species is exceptionally numerous in the above-mentioned vicinity. Hosts were collected also in January of 1932, and great masses of rediae were observed in the hepatic tissues. They were elongated sac-like structures (Fig. 26), only 0.263 mm. in length and 0.151 mm. in width in the immature stage, 2.25 mm. by 0.63 mm. in a more advanced stage and 3.42 mm. by 0.936 mm. in the case of large rediae containing developed cercariae.

The almost terminal, muscular pharynx contains noticeable cross-striations in its wall and is spherical in shape. The intestine is large and swollen in most cases (Fig. 24) and the cavity of the body is filled with what appears to be disintegrating tissues and small clear glandular bodies. No living cercariae were seen inside the rediae or in the tissues of the host in the snails collected in January, although, in a few cases, free cercariae were noted in the water after a mass of sporocysts had

been separated from the liver tissue. This may indicate that the length of infection is definitely limited, either by the seasonal factors or by the length of life of the rediae, both of which may result in such disintegration of the rediae in the liver tissue. Many of the rediae are greatly constricted in one, rarely in two areas (Fig. 25), giving the local region the appearance of a neck; also the posterior end, in many cases, is constricted, causing a posterior tail-like structure to be present. The intestine has never been observed extending into this portion.

When the snail hosts are kept in containers at room temperatures the cercariae emerge from them in greatest numbers between 8:00 and 9:00 in the morning. After this period very few leave the snail and in the late afternoon and evening the containers, with scarcely an exception, contain only encysted forms. On successive mornings this swarming is repeated, the snails often being so heavily infected with this form that the walls of the containers are literally covered with these cysts. After swimming about for a very short time they encyst on the glass, or preferably on water plants and sword grass, while the tail beats with great speed, then comes loose and swims about in the water for a long time before finally disintegrating (Fig. 21). The body rounds itself into a flattened circular body and a transparent, stiff covering is formed about it. The cyst is formed so rapidly that it resembles the molting process of some animals, but the substance of the wall is probably cystogenous material. By pressing on the cover-slip this cyst is broken and the worm crawls out. However, I have never observed it to reëncyst.

Almost all of the body is filled with small granules, refractile, and spherical or oblong, which make the cercaria appear almost black under the low power of the microscope. The body is also filled with pigment granules of a brownish or black color which make a detailed study of its structure from the living specimen very difficult if not impossible.

Probably the process of cyst formation is not a continuous one, for after the cyst wall has been formed it can be seen that there are several successive layers (Fig. 22). The body can rotate inside the cyst wall and twists about quite readily (Fig. 23). The following are averages of measurements on five specimens: diameter of cyst 0.232 mm., width of outer wall 28 μ, width of inner wall 28 μ, total width of cyst wall 56 μ.

The tail of the worm is relatively long, as long as the body while resting normally and much longer when extended for swimming. It has a parenchymatous core, and many striations are present which extend parallel to the core.

The body itself need only be characterized here, for its structure has been carefully studied by other workers. Many other very characteristic

features facilitate the identification of this cercaria, namely, the two relatively large, deeply pigmented eye-spots lateral to and almost on a level with the posterior limits of the oral sucker; the central eye-spot, slightly smaller, of a more brownish color, but also heavily pigmented; the condensation of pigment anteriorly and laterally; the elongate oval body, more pointed anteriorly and subquadrate posteriorly (Fig. 20). The narrow esophagus extends only for a very short distance posteriorly before dividing to form the two intestinal ceca which reach almost to the posterior end of the body and extend mesiad to the two large excretory vessels. The small excretory bladder is at the very posterior end of the body. The two excretory siphons are large, swollen, sinuous, and filled with small dark excretory granules (Fig. 20). Posterior locomotor appendages are on the posterior lateral margins of the body on either side of the tail base.

The two siphons which open into the excretory bladder, extend anteriorly on either side of the body, and unite in the region of the oral sucker, in the midline of the body, and just anterior to the median eye-spot. No other part of the excretory system could be distinguished in the body, but the tail contains a central longitudinal tubule which connects anteriorly with the bladder.

It is quite probable that the final host of this cercaria exists in some abundance in this stream, since such a high percentage of infection was found among the snails collected here. Furthermore, muskrats have been noticed several times along the banks and their holes are common in the banks. They are a likely mammalian host for this parasite, and since they are largely herbivores the metacercariae would have an easy method of gaining access into their bodies. This can be confirmed only by further studies.

Encysted forms or metacercariae were found fastened to the shell of the snail as well as on the bottom and sides of the container. The snails were collected on October 26, 1931, and most of the cysts contained living metacercariae on January 29, 1932. The cysts are circular objects, flat on their attached sides and convex on their outer surfaces. The coiled trematode can be seen clearly within (Fig. 23). It is deeply colored by a dark brownish pigment, only the anterior end being light in color. The worm lies in a central cavity and is separated from the cyst wall by a narrow space. The wall of the cyst is composed of layer upon layer of thin, clear homogeneous material. The animal within has elongated greatly and deepened in pigmentation. No trace of the two posterior locomotor appendages can be found, but the large granular excretory bladder is much larger here than in the free swimming stage.

VII. ECHINOSTOME CERCARIAE

History and Definition

In 1909 Lühe placed the Echinostome Cercariae in his Leptocercous Cercariae and characterized this Leptocercous Group as follows:

> Distome Cercarien mit ungegabelten und borstenlosem Ruderschwanze, dessen Breite auch im kontrahierten Zustande wesentlich hinter der des Körpers zurückbleibt.

Lühe designated three subgroups of leptocercous cercariae, one of which was the Echinostome Cercariae, and described the latter as follows:

> Ohne Bohrstachel. Vorderende mit einem ventral offenen, Kragenartigen Wulst, auf dem ein Stachelkranz zur Ausbildung gelangt.—Schlankschwänzige Cercarien von Distomen mit dem für die Echinostomiden charakteristischen, ventral offenen Kopfkragen, der auch schon bei unreifen, des Stachelkranzes noch entbehrenden Cercarien deutlich kenntlich ist. Reife Cercarien auch bereits mit Stackelkranz. Bohrstachel und Augen fehlen. Entwickelung in Redien, die einen vorderen Ringwulst, zwei hintere seitliche Fortsätze und eine sehr deutliche, dicht hinter dem Ringwulst gelegene Geburtsöffnung besitzen. Encystierung in einem Hilfswirt.

Sewell (1922) devised a rather extensive classification of the Echinostome Cercariae, in which he formed three subgroups: the Echinatoides, the Coronata, and the Echinata. He also included a fourth group of cercariae with the Echinostomes, the Megalurous Cercariae, because his study had convinced him of the relationship of this group to the Echinostomes. However, he does not submit findings which I believe constitute sufficient evidence for such a grouping, so I shall not discuss the megalurous cercariae at this time.

Many of Sewell's characteristics which he applies to the subgroups of Echinostomes can be equally applied to all of these subgroups so that definitive characters of these subgroups are obscured by generalities. Sewell also removed three cercariae from the Echinostome Cercariae since they had been described as having no collar spines, even though it had already been demonstrated that at least two of these individuals developed spines after encystment. I am speaking of *Cercaria agilis* Filippi 1857, *C. reflexae* Cort 1914 and the cercaria of *Himasthla militaris* Van Beneden 1861. He also described a new form without the collar spines, *C. indica* XLI.

Because of the above-mentioned difficulties in a grouping such as that of Sewell, I shall not attempt here to use his groups of Echinostomes. Furthermore, a definite designation of all the described larvae into subgroups seems inadvisable at this time. Several forms that have previously been listed as echinostome larvae must be removed from this group since new families have been created in recent years, such as Acanthostomidae Poche 1926, to include several of the old echinostome genera. Synonomy in the group is common. For instance, the cercaria of

Echinostomum revolutum has been considered by various authors to be *C. echinata* Siebold 1837, *Cercaria A* Tsuchimochi 1926, *Cercaria No. 7* Nakagawa 1915 and *C. limnicola* Faust 1924.

Faust (1924) attempted to divide these cercariae into ten subgroups according to their excretory systems, but such a grouping is impracticable for many forms whose flame cell formulae are unknown. Numerous cystogenous glands prevent accurate determination of the pattern of the excretory system in many echinostome cercariae.

The following forms have been described as possessing no collar spines:

1. *Cercaria agilis* Filippi 1857
2. Cercaria of *Himasthla militaris* Van Beneden 1861
3. *C. reflexae* Cort 1914
4. *C. fusiformis* O'Roke 1917
5. *C. arcuata* Cawston 1918
6. *C. complexa* Faust 1919
7. *C. penthesilia* Faust 1921
8. *C. indica* XLI Sewell 1922
9. *C. semi-robusta* Faust 1924
10. *C. pseudo-echinostoma* Faust 1924
11. *C. redicystica* Tubangui 1928
12. *C. chitinostoma* Faust 1930

The following forms do possess collar spines but they are all marine forms:

1. *Cercaria leptosoma* Villot 1879
2. *C. purpurae* Lebour 1907
3. *C. patellae* Lebour 1907
4. Cercaria of *Echinostomum secundum* Lebour 1912
5. *C. littorinae obtusatae* Lebour 1912
6. *C. quissetensis* Miller & Northup 1926

Descriptions of the following fresh-water forms do not include mention of a fin-fold on the tail:

1. *C. echinata* v. Siebold 1837
2. *C. echinatoides* Filippi 1854
3. *C. coronata* Filippi 1855
4. *C. spinifera* La Valette 1855
5. *C. number 7* Nakagawa 1915
6. *C. catenata* Cawston 1917
7. *C. trisolenata* Faust 1917
8. *C. chisolenata* Faust 1918
9. *C. acanthostoma* Faust 1918
10. *C. constricta* Faust 1919
11. Cercaria of *Echinostomum xenopi* Porter 1920
12. *C. cucumeriformis* Faust 1921
13. *C. indica* XX Sewell 1922
14. *C. indica* XII Sewell 1922
15. *C. indica* XXIII Sewell 1922
16. *C. indica* XLVIII Sewell 1922
17. *C. serpens* Faust 1922
18. *C. cristacantha* Faust 1922
19. *C. chekiensis* Faust 1924
20. *C. limnicola* Faust 1924
21. Echinostome Cercaria, *Species B* Tsuchimochi 1926
22. *C. hypoderaei conoidei* Mathias 1925
23. *C. isidorae* Faust 1926
24. *C. equispinosa* Brown 1926
25. *C. granulosa* Brown 1926
26. Echinostome Cercaria, *Species A* Tsuchimochi 1926
27. Cercaria of *Echinoparyphium flexum* McCoy 1928
28. *C. rebstocki* McCoy 1929
29. *C. mehrai* Faruqui 1930
30. Cercaria of *Euparyphium murinum* Tubangui 1932
31. *C. palustris* Chatterji 1933

Another form, unique along with *C. reflexae* in that it possesses a fin-fold on the tail, was described by Cort in 1914 as *C. trivolvis*. Three large-tailed echinostome cercariae have been described, unlike the other echinostomes in regard to their unique tails. They are *C. magnacauda* O'Roke 1917, *C. caudadena* Faust 1921, and *C. cita* Miller 1929.

Cercaria trivolvis Cort 1914

(Figs. 28-34)

Helisoma trivolvis appears to be particularly heavily infected with this form in Camp Creek near Seymour, Illinois, and in the St. Joseph Oxbow. *Physa gyrina* at St. Joseph, Illinois, was also infected.

The cercaria moves rapidly, either by crawling or creeping on a surface with its suckers or by a rapid lashing of its powerful tail, which is longer than the body when it is extended for swimming. The body is elongated, pointed anteriorly, and broadly rounded posteriorly. When contracted for swimming the body is 0.280 mm. long and the tail is 0.504 mm. long. When only mediumly contracted the body is 0.336 mm. in length. Under pressure it is 0.448 mm. by 0.280 mm. through the acetabulum. When extended the length of the body is 0.549 mm. and of the tail 0.616 mm. At its base the tail is 78 μ wide.

Under slight pressure narrow fin-folds are noted on the posterior half of the tail (Fig. 28). Without careful study it is impossible to see the very fine spines which are located on the anterior portions of the worm. A row of thirty-seven alternating spines partly encircles the body, with a break in the middle of the ventral surface. These spines are quite long, and point posteriad and laterad, except for the angle spines on the ventral surface near the edge of the break, which point toward the midline of the body.

The oral sucker and acetabulum of this distome are relatively far apart, with no very great difference in size. The length of the oral sucker averages about 65 μ and the width 69 μ when the worm is subjected to slight pressure. The acetabulum is 75 μ long and 80 μ wide. Both suckers are almost spherical. The oral sucker is followed by a prepharynx which is almost as long as the pharynx. The pharynx is 33 μ by 31 μ. The esophagus is long and reaches almost to the acetabulum, which is about 0.169 mm. posterior to the oral sucker. The two narrow intestinal crura reach almost to the posterior end. The entire esophagus and intestinal crura are filled with connected masses of tissue which enclose open spaces in what will later be the lumen (Fig. 28). This presents an unusual appearance in the living specimen and indicates that the digestive system is still non-functional. The acetabulum is about 91 μ from the posterior end of the body.

The excretory system is similar to that of most echinostome cercariae. Near the base of the tail on the dorsal side is the excretory pore, and just anterior to it is the small rounded excretory bladder. The two main collecting tubules, or excretory siphons, extend anteriad, and near the level of the anterior margin of the acetabulum they become greatly

swollen with large, uniform, spherical, two-layered, highly refractive excretory granules. These siphons lie intercecally and anterior to the oral sucker, the granules diminishing in number and size anteriorly, and ceasing in the region of the pharynx. The characteristic triangular loop of echinostome cercariae is present, and the tubules turn backward and continue posteriad, in the immediate vicinity of the siphon, almost to the posterior end of the ceca, before dividing into secondary tubules. One secondary tubule extends to the pharynx again before it branches to form capillaries. Flame cells were noted but it is difficult to determine their exact connection with the finer branches of the system because of the great number of characteristically dark cystogenous glands which fill the body except in the regions anterior to the pharynx and immediately anterior to the bladder. Another noticeable feature of this excretory system is the presence of vibratile elements, throughout almost the entire length of the descending siphons, particularly active in the region of the acetabulum and above it part way to the oral sucker.

One tubule extends posteriad into the tail, which soon divides into two lateral branches, each branch extending laterad to the very edge of the tail. Cort (1915) describes these branches as opening to the outside. However, I could detect no sign of an opening here. Perhaps these openings, functional in the early life of the undeveloped cercaria, become closed in the free-living form. Cort states that his material was often secured by dissecting the cercariae from the host tissue, and therefore it is possible that his material differed from emerged cercariae in some respects.

The body contains many large cystogenous glands which fill all available space in the body. Under pressure they can be seen to extend from the oral sucker, to the posterior end of the body, in four rather definite groups or rows. Two rows extend one on either side of the body, lateral to the main excretory tubes; an additional row on each side lies posterior to the pharynx between the esophagus and excretory siphon. They are interrupted by the acetabulum, but, posterior to it, continue to the end of the ceca. The space anterior to the bladder lacks these glands. Each gland is filled with elongated refractile bodies arranged in bundle-like formation.

Groups of glands, perhaps penetration glands, are posterior to the oral sucker, but distinct tubules connecting them with the anterior end of the body were not seen. However, a noticeable feature about this cercaria is a row of six swollen openings along the anterior lip of the oral sucker, each one of which extends posteriorly as a small fiber-like structure. Each fiber is swollen near the dorsal median side of the oral

sucker. Possibly each of these fibers is an undeveloped duct which connects with the penetration glands of the worm.

Masses of cells which are anterior and posterior to the acetabulum, and connected by a narrow row of cells, constitute the genital cell masses.

The tail is much longer than the body when extended for swimming, but under slight pressure is of about the same length. A core extends longitudinally through the tail, and the tissue next to this core contains a row of large, regularly arranged nuclei as shown by an optical section. They are easily seen in the tail when it is subjected to pressure (Fig. 34). A small fin-fold is limited to the distal part of the tail, and I believe this structure has never been described for other echinostome cercariae which have an anterior collar of spines. The posterior end of the tail tapers rapidly for a distance of about 0.114 mm., so that the posterior end is pointed. On some specimens there projects from this distal tip a tiny blunt projection, which is more evident with increased pressure, but which is only rarely seen. Ultra-microscopic projections or granules are present on this structure (Fig. 31) but its exact nature is not known. It is possible that it represents an inverted end of the tail which becomes evaginated under pressure (Fig. 32).

C. trivolvis develops in rediae which are transparent in the young stages but are yellow, and finally brown, in their later stages. The redia is elongated, with narrow posterior and anterior ends, but it varies greatly in shape according to the degree of extension of the body. Near the posterior end of the body are two prominent locomotor appendages, characteristic protrusions extending outward from the body wall and narrow at their distal extremities (Fig. 30). Posterior to these the body is narrowed, ending usually in a small knob-like extension, more prominent when the body is contracted.

Near the anterior end of the body, and a short distance posterior to the sucker, is a broad collar extending around the animal. When contracted, the sucker is partly withdrawn in this collar with only its anterior extremity showing (Fig. 33), but when fully extended a long slender neck separates the collar from the sucker.

Just posterior to the collar lies the lateral birth pore, and, under pressure, the cercariae are slowly expelled from the body through the pore (Fig. 29). Under these conditions the pore is situated on a slight prominence. The anterior opening of the cavity of the sucker is terminal, and posteriorly it opens into a rhabdocoele gut which is about one-half as long as the body. This gut is filled with dark material of a deep reddish-brown color, with the exception of its anterior extremity which is often transparent.

As the redia develops, its body cavity increases in size, even extending into the posterior locomotor appendages, and sometimes contains cercariae and germ balls in various stages of development.

Many of the immature rediae, when contracted, are only 0.347 mm. in length and 0.101 mm. in width, but when extended, measure 0.560 mm. by 62 μ. The mature rediae are about 0.878 mm. by 0.266 mm. but vary from 0.630 mm. to 0.170 mm. in length.

C. trivolvis emerges from its snail host in comparatively large numbers about noon of each day, probably due to temperature increases, but is present in the containers in decreased numbers during the night and early morning.

After swimming about for a time these cercariae enter their snail host again to encyst, or other snails if they are available. It has been found that host-specificity for the encysted cercariae is not very great for I have succeeded in recovering them from laboratory raised *Helisoma trivolvis, Physa gyrina,* Pseudosuccinea, and Succinea.

These cysts are transparent, and the worm coiled within is clearly visible. The spines are more easily discernible but the penetration glands are still indistinct.

During the summer of 1932, encysted forms of this cercaria were fed to a domestic duck which had been raised in a small pen where chances of trematode infection were minimized. Fourteen days after this time, the adult echinostomes were found in the intestine of the duck. Since it was impossible to continue the experiments at that time the experimental feeding was repeated on a more extensive scale during the summer of 1933.

On July 9, 1933, laboratory raised *Physa gyrina* and one *Helisoma trivolvis* were placed in a container with a *Helisoma trivolvis* from St. Joseph which was giving off *C. trivolvis* in large numbers. On July 14 these six snails were examined and a number of encysted forms were found in each. This material was then fed to a three months old duck. On July 28 the duck was examined and twenty-seven large echinostomes were found at the lower end of the alimentary tract attached to the walls of the tract just inside the anus.

Later the experiment was repeated; this time five small *Physa gyrina* and two *Helisoma trivolvis,* all laboratory raised, and previously exposed to emerging cercariae, were fed to a young duck about three and one-half months old. Cysts in one snail were counted and twenty-six were found. After sixteen days mature echinostomes were recovered from the duck.

Further studies are in progress concerning this life history and the identification of the adult, and will be given fully in a later discussion of its life history.

VIII. XIPHIDIOCERCARIAE

Definition

The cercariae commonly termed xiphidiocercariae represent an immense number of forms, differing greatly in their anatomical structure but all having at least one structure in common, namely a stylet. However, it must be borne in mind that other forms not placed in this group also have stylets, for instance, the microcercous and gorgoderine cercariae. Nevertheless, in the xiphidiocercariae this stylet possesses a single sharp point and sometimes a bulb-like swelling, while in other forms the stylet sometimes assumes a complex structure with several points along a ventral border, for example in the gorgoderine cercariae.

Several authors have described the act of penetration into new hosts when the cercaria uses the stylet to make an aperture in the tissue, so that we must conclude that this often functions as a definite penetrating structure.

All members of this large group also possess certain glands, and, as they seem to have no connection with the stylet, I am using the term *penetration gland* which better expresses their true nature. The various formations which these glands may assume, as well as the nature of their usually granular contents, are convenient features for specific diagnosis, and workers have utilized this characteristic even for the designation of subgroups (Sewell, 1922).

Lühe (1909) defined the xiphidiocercariae as follows:

> Schlankschwänzige Cercarien von Distomen mit einem Bohrstachel am abgerundeten Vorderende. Augen fehlen. Entwicklung in Sporocysten. Die Encystierung erfalgt in einem Hilfswirt. Hierher besonders zahlreiche und schwer zu unterscheidende Arten.

The xiphidiocercariae have been subsequently divided into a number of groups, the members in each case showing certain structures in common which authors have recognized as showing probable relationship. Lühe (1909) recognized only four such groups: Cercariae Microcotylae, Cercariae Virgulae, Cercariae Ornatae, and Cercariae Armatae. Lebour (1911) placed some forms in a new group, the Spelotrema, and Cort (1915) created another, the Polyadenous Cercariae.

Cercariae Ornatae

History and Definition

Lühe (1909) created the group Cercariae Ornatae to include two species, *Cercaria ornata* La Valette 1855 and *C. prima* Sinitsin 1905, and characterized it as follows: "Distome Cercarien mit Bohrstachel, deren schlanker Ruderschwanz einem Flossensaum besitzt."

Later Cort (1914) added *C. hemilophura* to Lühe's Cercariae Ornatae.

Sewell (1922) created a new subgroup, the Prima group, for his two new species *C. indica* XXIV and *C. indica* XXVIII and defined the group as follows:

(1) Distome Cercariae of moderate size in which the acetabulum is smaller than the oral sucker and is situated behind the middle of the body-length.
(2) The tail is shorter than the body and is furnished with a dorso-ventral fin-fold in its distal portion: the ventral portion of the fin extends further forwards than the dorsal part.
(3) The alimentary canal possesses a prepharynx and a pharynx and the intestinal caeca reach back to a point between the posterior margin of the acetabulum and the posterior end of the body.
(4) Salivary glands are present, and consist of four or five pyriform cells.
(5) The excretory bladder is oval or rectangular and the main excretory canals are dilated in the posterior part of their course and open into the bladder by a common median orifice. The excretory formula appears to be $2 \times 6 \times 1 = 12$ flame-cells.
(6) Development occurs in oval or sack-shaped sporocysts.

Faust (1924) made a second subgroup, the Hemilophura, on the basis of the excretory system, and placed *C. hemilophura* Cort 1914 and *C. trifurcata* Faust 1919 in it. He considered both these forms to have the flame cell formula $2\ [(3 + 3) + (3 + 3 + 3)]$. However, McCoy (1929) found that *C. hemilophura* does not possess this formula and said it should be removed from the Hemilophura. Thus we have a third subgroup differing from the original two in having an excretory system of the $2\ [(3 + 3 + 3) + (3 + 3 + 3)]$ type. To this I shall add one species described below, namely *Cercaria mesotyphla.*

Since the above groups have been based largely on the character of the excretory system, it leaves out of consideration one species of ornate cercaria, *Cercaria racemosa* Faust 1917. Faust did not give the details of the excretory system of this form, but the system is obviously quite different from that of other forms of this group. Therefore, it must be placed in another subgroup. There are naturally many questions about such a classification as has been made for this group of cercariae, but perhaps the above will serve to show the morphological distinctions which various authors have pointed out for different individuals of the Cercariae Ornatae.

At present the group comprises the following:

Subgroup 1. Prima Group Sewell 1922.
1. *C. ornata* La Valette 1855
2. *C. prima* Sinitsin 1905
3. *C. indica* XXIV Sewell 1922
4. *C. indica* XXVIII Sewell 1922
5. *C. longistyla* McCoy 1929

Subgroup 2. Hemilophura Group Faust 1924.
1. *C. trifurcata* Faust 1919

Subgroup 3.
1. *C. hemilophura* Cort 1914
2. *C. mesotyphla* E. L. Miller 1935

Subgroup 4.
1. *C. racemosa* Faust 1917

Cercaria mesotyphla E. L. Miller 1935

(Figs. 35-40)

Physa gyrina hildrethiana from the Oxbow at Muncie, from Camp Creek at Seymour, and from East Lake Fork near Sadorus, were infected with *C. mesotyphla*. Also *P. halei* from Alhambra and *P. gyrina* from the Oxbow at St. Joseph and a Pond near Rantoul were parasitized by this form. Infection is quite prevalent in the Urbana region and was particularly high at Rantoul. Hall, in a personal communication, reported the same cercaria from the Embarrass River near Urbana.

In appearance the body is an oval, narrowed in front and more bluntly rounded behind. It is a rapid swimmer and the tail lashes violently from side to side as it propels the body. In regard to its emergence from the host, Hall also states that under constant conditions of light, daylight, and temperature of fifty degrees F., the numbers of cercariae given off are constant, being approximately two hundred over a twenty-four hour period. A decreasing in the amount of light and temperature causes the number of cercariae given off to decrease proportionately.

The body is rather small, being only 0.35 mm. long and 0.308 mm. wide through the acetabulum when contracted. In the same state the tail is 0.308 mm. long. When well extended the body is 0.576 mm. by 0.196 mm. and the tail is 0.616 mm. long, and 0.308 mm. wide near its base.

Spines cover the entire body and are directed posteriorly, being more dense near the anterior end of the body.

The tail is smooth and without a lumen; it possesses a noticeable fin-fold near its posterior half (Fig. 35) which decreases in width near the posterior end. It is attached to the body on its ventral surface, just anterior to the posterior end of the body. It is quite muscular and has longitudinal muscles which are evident when subjected to pressure. There are four groups of these longitudinal muscles which extend in wide spirals through the tail, in addition to a deeper circular layer. It will be seen from the above measurements that the tail is as long as, or slightly longer than, the body of the worm (Fig. 35). The fin-fold extends along the distal two-thirds of the tail.

The acetabulum is slightly posterior to the middle of the body and is smaller than the oral sucker. It is circular and measures 60 μ in diameter, when the body is slightly contracted, while the circular oral sucker measures 84 μ in diameter.

The cavity of the oral sucker opens into a short prepharynx, about 40 μ long, which connects with a thick-walled, muscular pharynx. This structure is 44 μ wide when it is contracted and only 40 μ long. The

esophagus extends posteriad for a distance of 50 to 80 μ and then divides to form the intestinal ceca which reach almost to the posterior end. On the posterior border of the intestinal fork is a noticeable bulge or sac, which persists, to a lesser degree, even when the worm is greatly extended (Fig. 35). This is a characteristic feature of this species.

The stylet points forward and toward the dorsal lip of the oral sucker, and is comparatively small, being only 23 μ in length. It has a clear hyaline base and its walls are thick, particularly in the region of its posterior third, and in the anterior portion just behind the point (Fig. 39).

Lateral to the esophagus, on either side, lies a group of six stylet glands, each of which opens through an individual duct. These glands are particularly indistinct in this species. The main duct which leads anteriad from each group of glands is bipartite in nature. After reaching the region of the stylet it opens above and anterior to the cavity of the oral sucker. These glands do not take neutral red stain as readily as do those of most other forms which I have examined. Many other glands are present in the body, particularly from the acetabulum to the oral sucker and along the sides of the body.

Dorsal to the ventral sucker are two groups of cells, the germ masses. Both masses lie in a diagonal, dorso-ventral plane and their upper ends are narrowed (Fig. 40). This narrowed portion may indicate the beginning of an accessory duct, the oviduct or the vas deferens, since the masses may represent the ovary and testes of the adult.

A body which I believe is a ganglion of the nervous system lies on either side of the pharynx, but the nerves could not be distinguished.

The excretory system is characterized by two spherical bladders, an anterior and a posterior one, which fill and empty in a rhythmic manner, and by a flame cell formula of the 2 $[(3+3+3)+(3+3+3)]$ type (Fig. 36). The two alternately contracting bladders, when filled with fluid, are slightly different in size, the upper being about 40 μ wide and 20 μ long, and the lower 30 μ wide by 19 μ long. When the contents of the posterior bladder are expelled through the pore, the anterior bladder empties its contents through the median constriction, the process being repeated rapidly when little or no pressure is exerted on the worm.

The two main collecting tubules proceed anteriad and just anterior to the acetabulum they divide into an anterior and a posterior branch.

The anterior branch on each side gives rise to three branches, one in the region of the cecal bifurcation, one lateral to the esophagus, and one lateral to the pharynx. Each of these branches divides dichotomously into three capillaries, each ending in a flame cell, the location of which can be ascertained by examining the illustration (Fig. 36).

The posterior branch on each side gives rise similarly to three groups

of flame cells, three in each group, its first division being just posterior to the acetabulum, the second opposite the anterior bladder, and the third lateral to the constriction between the two vesicles of the bladder. Of course the locations of the divisions of the tubules vary slightly with contraction, but the locations of the flame cells are constant.

The above flame cell formula shows why I believe this species should be placed in a subgroup of the Cercariae Ornatae along with *C. hemilophura* Cort 1914.

The sporocysts of *C. mesotyphla* are long, slender sacs of a brownish-yellow color, and vary in size. The larger ones measure about 5.70 mm. in length by 0.43 mm. in width and the smaller ones 3.60 by 0.36 mm. Very little liver tissue of the host remained but great tangled masses of sporocysts were present. They were twisted almost inextricably about one another (Fig. 37), each one having one free end while the other end was attached to the central mass. The free end often moves slowly back and forth, resembling some algae in this respect, and even contracts and extends, although not to any appreciable degree.

Each sporocyst contains cercariae and germ balls in various stages of development (Fig. 38). The structure of the immature cercaria is difficult to see because of many small dark cells which crowd its entire body. Those forms having the ability to move about in the sporocyst were very active. No birth pore was noted in the sporocyst.

Dissection of *P. gyrina* from Rantoul, Illinois, disclosed the presence of an infection with cercariae which are identical with the above form in all characteristics which I have noted. However, the sporocysts presented some differences. All five infected snails in this lot contained numerous short sporocysts about 0.592 mm. long by 0.200 mm. wide. This might indicate that these are fairly young sporocysts, even though some of them contained a few mature cercariae.

After living more than thirty hours in tap water these cercariae still failed to encyst. All attempts to make them encyst upon minnows, gold fish, tadpoles, crayfish, and water plants were unsuccessful. I have also attempted to cause their encystment upon isopods, giant water bugs, and whirligig beetles from the regions of infection, but all attempts were unsuccessful. Many dead cercariae were noted in the same containers with these possible intermediate hosts, but no cysts were found.

Because the cercaria is so similar in structure to the adult trematode, *Glypthelmins quieta* Stafford 1900, and particularly because its excretory system is identical to that of *G. quieta* which I illustrated in an earlier publication (1930), I thought that it might prove to be the larval form of this trematode. My findings have shown that both this larva and the adult *G. quieta* occur commonly together in different localities in Illinois.

The only species with which *C. mesotyphla* might be confused is *Cercaria hemilophura* Cort 1914. The fin-fold of *C. mesotyphla* is consistently longer than in Cort's form, *C. hemilophura;* Cort says the whole body of *C. hemilophura* contains small cystogenous glands which fill almost all available space, but I do not find these in *C. mesotyphla;* Cort also said he could not distinguish stylet glands in his species; the bladder of *C. hemilophura* is club-shaped but has two vesicles in *C. mesotyphla;* and no blind pouch between the ceca has been described for *C. hemilophura.* The measurements of *C. hemilophura* differ from those of *C. mesotyphla.*

Cercariae Microcotylae

History and Definition

Sewell (1922) believes these forms represent the most primitive of the xiphidiocercariae. Lühe used the size of these minute forms to separate them in his key, but since it is impossible to place many intergrading forms which have been more recently described, authors have found it necessary to disregard the size element. However, there are other characteristics for the group which aid in a classification of these forms. The great majority of them have no digestive system posterior to the pharynx and the rest have only very short intestinal ceca.

Lühe (1909) listed ten species of microcotylous cercariae and defined the group as follows:

> Sehr kleine distome Cercarien mit schlakem ungegabeltem Schwanz und mit Bohrstachel. Körperlänge unter 0.2 mm. Bauchsaugnapf wesentlich kleiner wie der Mundsaugnapt und hinter der Körpermitte gelegen. Stacheldrüsen gering an Zahl (2-4), dicht neben und vor dem Bauchsaugnapf gelegen, häufig von gelblicher, bräunlicher oder grünlicher Farbe. Exkretionsblase klein, mit am verbreiterten Vorderende mehr oder weniger deutlich hervortretender Gabelung. Hautbestachelung bisher nur bei egyptischen Arten nachgewiesen, aber wahrscheinlich auch bei deutschen Arten vorhanden.
>
> 3 deutsche Arten scheinen durch verschiedene Form des Bohrstachels sichergestellt, einige weitere sind unsicher.

Cort (1915) improved on the above characterization:

1. Developed in gastropods in round or oval sporocysts which are seldom more than twice as long as wide.
2. Cercariae under 0.2 mm. in length.
3. Acetabulum back of the middle of the body and smaller than the oral sucker.
4. Stylet glands not more than four on each side and arranged in rows on each side of the acetabulum.
5. Digestive system undeveloped except for a short prepharynx and a small pharynx.

Sewell, working in 1922, divided these forms into four subgroups, namely the Cellulosa, the Pusilla, the Parapusilla, and the Vesiculosa. However, the separation of these subgroups by Sewell's superficial characters is questionable.

Cellulosa Subgroup

Although Sewell (1922) first used this term and placed in the subgroup *C. cellulosa* Looss 1900 and *C. indica* LVII Sewell 1922, he failed to characterize the subgroup, other than to say: "The possession of only two salivary-gland cells on each side of the body and the simple structure of the excretory system, comprising only four flame cells on each side of the body, appear to me to be sufficient grounds for creating a new sub-group for this form." Probably the following forms also belong to this subgroup: *C. chlorotica* Diesing 1850, *C. brunnea* Ercolani 1850, *C. microcotyla* Filippi 1854, and *C. pseudornata* Lühe 1909.

I have studied three species of microcotylous cercariae which belong to this subgroup:

Cercaria cystorhysa E. L. Miller 1935

(Figs. 41-46)

Collections of *Goniobasis livescens* from the Salt Fork River at Homer, Illinois, in May, 1932, were found to yield large numbers of tiny stylet cercariae, for which I proposed the name *Cercaria cystorhysa* in 1935.

A number of features make this form unique among local cercariae. It is very minute and not easily seen with the naked eye, being only about 0.140 mm. in length even when extended as it crawls along with the aid of its suckers beneath the cover-slip. During such movement the tail is pulled along without beating from side to side—a characteristic of many stylet cercariae—so that its surface is contracted into folds. The tail is not more than one-half of the body in length when they are both at rest and it approximates more nearly a third of the body when they are contracted (Fig. 41).

Ordinarily the body of the worm is about 0.140 mm. by 34 μ when extended and 73 μ by 56 μ when contracted. However, when the extended worm is quieted by the application of pressure it is 0.140 mm. by 50 μ.

The tail is 39 μ long when contracted and 0.140 mm. when extended, but with pressure it is about 43 μ long and 23 μ wide at its base.

The longitudinal diameter of the oral sucker is 30 μ and the transverse is 27 μ while the acetabulum is about 18 μ in diameter. These measurements were taken when the worm was at rest. The acetabulum is located at a point about 33 μ posterior to the posterior margin of the oral sucker, and it is 39 μ from the posterior end of the body.

When swimming, the body is contracted and bent ventrally while the tail lashes back and forth in a jerky, spasmodic movement. After

swimming for a time the cercaria settles to the bottom of the container where it remains until death.

The body is elongated and flattened, and the ends are both broadly rounded, with the anterior narrow and the posterior subquadrate. No body spines were noted on this form.

A well-developed oral sucker and acetabulum are present, but the latter is posterior to the middle of the body and noticeably smaller than the oral sucker, being from one-half to two-thirds of it in size. It lies at a point about two-thirds of the body length from the anterior end of the worm.

A central lumen or core is seen in the tail when no pressure is applied, resembling that of other microcotylous cercariae in this respect. Strong pressure and oil immersion enabled me to see numerous tiny hair-like structures on the distal third of the tail (Fig. 44). A few large, deeply-stained nuclei are scattered through the tail.

Located dorsally and in the anterior end of the body is a relatively large stylet about 17 μ in length. It has the characteristic swelling, a swollen circular ridge, at a distance of two-thirds its length from the base of the stylet. The thickened stylet wall does not extend entirely to the base of the stylet, but only a thin membrane surrounds this portion (Fig. 43).

Lateral to the acetabulum on either side of the body is a pair of penetration glands differing from each other in shape and in the nature of their content. The outer gland is more elongate; it consists of three lobes or parts but has only one nucleus, and it takes neutral red stain readily. It is granular but cannot be seen clearly without the application of pressure. The inner gland is more compact, non-lobed, and contains a large spherical nucleus (Fig. 41). The salivary duct, which contains a granular fluid similar in appearance to that of the two median penetration glands, and which is swollen at irregular intervals, passes forward, above the oral sucker. These ducts open, one on either side of the stylet, where granular material exudes, under pressure of the cover-slip. This material adheres to the body surface and remains there as globules for a long time.

Many nuclear bodies are scattered through the outer tissue of the body and stain darkly with neutral red.

Posterior and to the left of the acetabulum is a crescent-shaped mass of tissue which stains a light pink in neutral red; it is probably the primordium of the reproductive system of the adult worm.

The excretory bladder is small and approximately rectangular when not swollen with fluid. This bladder is prolonged laterally where it gives rise to the main collecting tubes of the excretory system. A characteristic

feature of this bladder when only partially filled is its possession of anterior and posterior folds or wrinkles (Fig. 42). During contraction this bladder is rectangular but becomes U-shaped when the body is extended. The folds give a great variety of shapes and sizes to the bladder.

The course of the main collecting tubule on each side becomes lost in a coiled mass of tubules just anterior and lateral to the bladder, but an anterior continuation is present, which soon divides into two branches, the anterior of which extends to the region of the oral sucker (Fig. 42). The minute size of this form made it impossible for me to work out the location of the capillaries and terminal cells.

Cercaria cystorhysa matures in small, oval, or sac-like sporocysts which occur in great masses (Fig. 46) in the liver tissues of *Goniobasis livescens.* They are grayish or semi-transparent in color and are filled with granules and small globules. They vary in shape from spherical to oblong, many possessing knob-like projections at one end, while some are irregular in outline, with constricted centers. An average of eight sets of measurements shows the oblong forms to be 0.195 by 0.121 mm., the oblong forms with knobs to be 0.187 by 0.116 mm., those forms with constricted centers to be 0.174 by 0.101 mm. and the spherical ones to be 0.126 by 0.112 mm.

Mature cercariae move about inside, but in no case were they seen to escape through the walls. No birth pore was noted.

No sporocysts were found which contained more than four cercariae, and I have never seen more than two fully developed ones in a sporocyst (Fig. 45). Only one cercaria was found in many of them, but in such cases the snail hosts had been kept in the laboratory for nearly three weeks before they were examined.

Cercaria meniscadena E. L. Miller 1935

(Figs. 47-51)

The percentage of infection is higher for this species than for any other found in Illinois. Large numbers of *Pleurocera acuta* Raf. were collected in the Sangamon River near Mahomet, Illinois, in October, 1931, and found to be heavily infected with *C. meniscadena.* Pleurocera from Oconomowoc River, Wisconsin, was also infected with this cercaria.

The worm crawls with the current under the cover-glass, and moves by extending its anterior end and contracting the posterior end as it is pulled forward. It progresses slowly in this manner, the tail being of no use. When free in the water it has the characteristic, jerky movement of the microcotylous cercariae and moves its body and tail violently.

Later it falls to the bottom of the container, where it rests, congregating there in great numbers.

The body is elongated with a broadly rounded anterior and a narrow posterior end where it is only 18 μ in width. In the region of the penetration glands and acetabulum the width increases. When well contracted the body is about 89 μ long by 66 μ wide. This width was taken through the acetabular region. The tail, at the same time, is 59 μ in length by 16 μ in width near its base. When well extended for movement the body is 0.170 mm. long and the tail 0.150 mm. When at rest the body is 0.117 mm. by 52 μ and the tail is 78 μ by 17 μ. When under pressure of the cover-slip, and slightly contracted, the body is 0.143 mm. by 72 μ and the tail is 0.117 mm. by 17 μ. When well contracted the body and tail together measure 84 μ in length, when at rest about 0.124 mm., and when greatly flattened by pressure 0.224 mm. It can be seen that the tail is only slightly shorter than the body, whether the cercaria is contracted or extended (Fig. 47).

No spines can be definitely determined for this form; however, under immersion oil, granular-like objects can be noted over the body surface.

The oral sucker is well developed and much larger than the acetabulum, which is a little posterior to the center of the body. The oral sucker is slightly wider than long, being 33 μ in transverse and 30 μ in longitudinal diameter. The acetabulum lies about 39 μ posterior to the oral sucker and is 20 μ in diameter. It is about 52 μ from the posterior end of the body. The oral sucker's cavity empties into a tiny pharynx. No prepharynx is present and only a tiny portion of the esophagus was seen. The remainder of the digestive system has never been observed.

The stylet, in the anterior lip of the oral sucker, is 17 μ long and 5 μ wide at its base, while the pointed tip at its anterior end distal to the swollen ridge is 5 μ long (Fig. 47).

Two large penetration glands are on each side of the body, the anterior one being in front of the acetabulum and the other being lateral to it. The anterior gland is darker and more coarsely granular, evidently containing a substance of a different nature. Each gland contains a large clear nucleus. Indistinct bipartite ducts lead forward to the region of the stylet, where they open to the outside. Lying on each side of the body, between the ventral sucker and the two salivary glands, is a transparent body which cannot be seen without great pressure. It presses against the salivary glands, during contraction of the body, and gives to the posterior pair especially, a crescent shape. The transparent body contains a single large nucleus. Perhaps this body is a very early stage of the reproductive glands.

The small excretory bladder is rectangular when not fully expanded,

but when extended it is U-shaped, due to the expanded proximal portions of the two main collecting tubes. Its pore opens to the outside on the dorsal surface. In side view this bladder is seen to have considerable thickness; it measures approximately 26 μ in width and 10 μ in length when expanded.

The two horns of the U-shaped bladder soon narrow into very fine tubules which are so minute and tangled in this cercaria that I was not able to see the connections of their branches with certainty. However, the main collecting tube can be seen to divide in the region of the acetabulum into a posterior and an anterior branch. A division occurs in the anterior branch in the region of the salivary glands. No part of the excretory system could be seen extending into the tail.

The tail has thick walls and a large lumen in its center. Annular constrictions, which are often present even when the animal is greatly extended, characterize it. At times the constrictions are annular, particularly when the tail is greatly contracted (Fig. 48); again they remind one of spirally twisted ridges extending around the tail. During extension these rings disappear at the base of the tail, the smoothing process continuing up to the distal end. About 13 μ from its distal end is a small vesicle which sometimes appears when the worm is subjected to pressure.

C. meniscadena develops in small, swollen, oblong sporocysts which are characteristic of the cercariae of the Cellulosa subgroup. They are massed together in the liver of the host, particularly near its surface.

The ends of the sporocysts are bluntly rounded, so that they have an oval appearance in most cases. The nearly colorless wall is very uneven in its thickness, being very thick in some places, while in others it is very thin but extremely tough (Fig. 49). A central cavity is filled with fluid and contains an abundance of small spherical bodies. Loose strands of tissue are also present in the cavity.

Commonly one, two, and three cercariae are found in the sporocysts, while germ balls are also present (Fig. 50). In many cases disintegrating germ masses are observed. Many sporocysts were also found that contained neither germ balls nor cercariae.

These sporocysts have no power of independent movement, at least in their older stages. Mature cercariae move about for hours, pushing the immature individuals aside in their progress, but none were seen to rupture the sporocyst's wall.

The sporocysts vary greatly in size and shape; however, all are approximately oblong or spherical, many with median swellings or terminal knobs (Fig. 51). The average sporocyst is about 0.185 mm. long and 0.124 mm. wide. Fifteen specimens were taken at random for this

average. The oblong ones average about 0.205 mm. by 0.127 mm. and the more spherical ones 0.154 mm. by 0.120 mm. Two or three cercariae or germ balls were noted in most of the sporocysts but in the majority of cases only one fully developed cercaria was found.

Attempts to induce the free swimming cercariae to encyst in crayfish were not successful. No cercariae were found encysted in the tissue of the snail host.

Cercaria cyclica nov. sp.

(Figs. 52-53)

A number of snails of the species *Viviparus georgiana* at Leesburg, Florida, were examined in October, 1931, for cercarial infection and two were found to be infected with a very small stylet cercaria, for which I propose the name *Cercaria cyclica.* It is the smallest cercaria that I have studied, the body being only 0.126 mm. long when slightly extended and 66 μ wide through the acetabular region, while the length of the tail is 0.126 mm. When extended for movement the body measures 0.143 mm. by 52 μ and the tail is 0.124 mm. long and 18 μ wide near its base.

The worms emerge from the snail in large numbers in the early morning but emergence soon ceases until the following morning when there is another swarming. The body is elongate in shape with a subquadrate posterior end, but becomes circular in shape almost immediately when placed on a slide for study (Fig. 52), so that it is impossible to study it in its normal, free-living shape. This circular shape is quite characteristic, for in less than one minute it has rounded into a flattened circle for encystment.

The stylet works incessantly at this time, evidently trying to break through the cover-slip. The tail is lost when encystment begins, and soon it becomes inactive. The worm is an active crawler and makes good use of its suckers. No body spines were seen.

The oral sucker is large, being slightly more than twice the size of the ventral sucker, which is posterior to the middle of the body on a small projection. No part of the digestive system posterior to the cavity of the oral sucker was noted in this form.

The tail is of about the same length as the body; a central cavity extends through its center but no part of the excretory system could be seen in it.

Many small globules are located mainly in two areas of the body, one area being just posterior to the large stylet glands and the other smaller area immediately posterior to the oral sucker.

The worm has an unusually large stylet in proportion to the size of its body, the stylet being 20 μ long and 5 μ wide at its base. The swol-

len area or shoulder near its anterior end is also very prominent and well developed (Fig. 52).

Perhaps its most noticeable features are the penetration ducts on each side of the body. In this form there are really two ducts on each side which are not even connected as are the components of the bi- and tripartite ducts of several other forms. The outer, lighter, and finely granular duct opens anterior to the other, and connects posteriorly with a large elongated penetration gland which lies in a transverse position just lateral to the acetabulum. When the body is contracted this gland becomes folded, since its anterior end merges gradually into its duct, giving the appearance of two glands instead of one. The diameter of this duct is not at all uniform, and at one point, about midway in its course, it is swollen into a large, gland-like body, which contains a nucleus similar to that in the gland proper. For this reason two of these glands may be considered to be on each side, instead of only one.

The median duct on each side contains larger droplets of material different from that in the other duct. Anteriorly it ends slightly behind the anterior end of the other duct, and posteriorly it widens into a large body just anterior to the acetabulum (Fig. 52). The two inner ducts both connect to this median enlargement.

A small rectangular bladder, which becomes U-shaped when the body is extended, due to its swollen lateral projections, gives rise to the main collecting tubes. Posterior and lateral to the acetabulum each of these tubes divides into an inner secondary tubule which divides into three branches near the acetabulum, and an outer secondary tubule which divides into a posterior and an anterior branch (Fig. 53). The anterior branch is greatly convoluted anterior to the acetabular level, but finally continues, dividing into three terminal branches lateral to the acetabulum. I believe these are the capillaries of the excretory system but I have never observed flame cells in this form.

After removal of these forms from containers each formed a cyst wall. Tapping on the cover-glass caused this wall to break and the worm to crawl out. However, I have never observed these forms to encyst a second time, for they always died soon after leaving the broken cyst wall.

Cercariae Armatae

History and Definition

Lühe in 1909 placed a number of xiphidiocercariae in this group because these forms are without a fin-fold and the body length reaches over 0.25 mm. He described the group as follows:

Distome Cercarien mit Bohrstachel, deren schlanker Ruderschwanz keinen Flossensaum und ungefähr dieselbe Länge wie der Körper besitzt. Körperlänge 0.25 mm. überschreitend. Bauchsaugnapt etwas hinter der Körpermitte gelegen und, wenn über haupt, so doch meist nur wenig an Grösse hinter dem Mundsaugnapt zurückbleibend. Exkretionsblase (soweit bekannt) Y-förmig.

Hierher anscheinend sehr zahlreiche und schwer zu unterscheidende, bisher offenbar auch erst zum kleinen Teil unterschiedene Arten.

Perhaps Lühe's statement that the species of this group are based on small differences, indicates the confusion met with in a study of the classification of these species. He listed ten species as belonging to the group but since then many more have been added.

Cort (1915) created a new group of xiphidiocercariae and gave it the name Polyadenous Cercariae, but Sewell (1922), recognizing the fact that size does not constitute a logical basis for cercarial groupings, considered this a subgroup of the Cercariae Armatae, in spite of the small size of the two forms which Cort placed with the polyadenous cercariae, namely *C. isocotylea* Cort 1914 and *C. polyadena* Cort 1914.

Later Sewell divided the Cercariae Armatae into two subgroups, the Polyadenous Cercariae Cort 1914 and the Daswan subgroup Sewell 1922. Sewell modified Cort's definition of the polyadenous cercariae and gave several characteristics of his Daswan subgroup, but the majority of these characters apply equally to both subgroups. However, the forms which Sewell placed in these subgroups, including his new species, do not follow his own definitions of the subgroups, the result being, so far as I am able to determine, that only two points in these characterizations are sufficiently constant to form a working basis for the assignment of species to them, namely, (1) that referring to the development of the cercariae in elongate sack-shaped or filiform sporocysts in the case of polyadenous cercariae and in sausage-shaped sporocysts in the case of those of the Daswan Subgroup, and (2) the character of the excretory tubules in the two groups.

Even here these two points are highly problematical, for many authors have not described or figured these sporocysts, and secondly, the character of the excretory system in these minute forms is of such a nature that it has never been described in the majority of forms and probably never will be in many of them because of cystogenous and penetration glands which make it impossible to locate already obscure flame cells and capillaries.

Altogether there have been well over fifty of these Cercariae Armatae described from various parts of the world. At least twelve species from the United States have been sufficiently described so that they can be definitely assigned to this group. The list is as follows:

1. *Cercaria polyadena* Cort 1914
2. *C. isocotylea* Cort 1914
3. *C. haskelli* O'Roke 1917
4. *C. gregaria* O'Roke 1917
5. Cercaria of *Lissorchis fairporti* Magath 1917
6. *C. crenata* Faust 1917
7. *C. glandulosa* Faust 1917
8. *C. diaphana* Faust 1917
9. *C. dendritica* Faust 1917
10. *C. micropharynx* Faust 1917
11. *C. stilifera* Faust 1918
12. *C. candelabra* Faust 1919

Several species of Cercaria Armatae have been found commonly in the Urbana area, as well as at Leesburg, Florida, and Baton Rouge, Louisiana.

Cercaria acanthocoela E. L. Miller 1935

(Figs. 54-59)

This species was found in *Helisoma trivolvis* from a variety of places, chiefly in the Oxbow at Urbana, the Pollywogs and Oxbow at St. Joseph, and Camp Creek at Seymour, Illinois. It was also found in *P. gyrina hildrethiana* from Camp Creek, Seymour.

It does not remain active for any length of time but soon falls to the bottom of the container where it can be found crawling about among the débris. In swimming, the entire body is twisted from side to side, the tail lashing even more rapidly, the result being an aimless movement, jerky and unsteady, which does not favor rapid movement in any one direction for long. When in motion the body is bent into a loop with the dorsal side outside, and the entire body is somewhat contracted. When it comes in contact with any hard object such as the walls or bottom of the container, it progresses by means of its suckers, and, if a cover-slip is above it, it prefers to crawl with its ventral side uppermost. As it moves in this manner, the contracted tail is dragged along behind the body.

The body is small and oblong in outline (Fig. 55) with its greatest width through the region of the acetabulum when at rest. However, the worm has great powers of extension, extending sometimes until it resembles a long narrow ribbon. When greatly contracted it may be more subquadrate in shape. When subjected to pressure it contracts, the anterior region becoming much wider while the posterior end becomes very narrow. The anterior end is rather bluntly rounded because of the subterminal position of the oral sucker, while the posterior end has pronounced rounded corners because of the presence of setae pockets or caudal pockets on either side of the tail base. When contracted the body is 0.228 mm. in length and 0.111 mm. in width, but when extended it measures 0.355 mm. in length, 85 μ in width. Its length is 0.252 mm. when it is at rest. Neutral red was added to the water to quiet the cercariae and then measurements were taken with little difficulty.

The body is armed with large spines which are situated in rows that run horizontally and diagonally across the body. The spines at the anterior end are quite pronounced but they decrease in size and become more scattered posteriorly, until posterior to the acetabulum they are very small and far apart.

The body wall extends ventrally on either side of the tail, which is attached on the ventral side of the animal near the end of the body. Because of these lateral processes of the body wall, a setae pocket is formed on either side of the tail base, so named because it is open at its anterior end and bears a group of long setae, or spine-like processes, clearly evident from either a dorsal or ventral view (Fig. 54).

The oral sucker is slightly larger than the acetabulum, being 67 μ in diameter when at rest while the acetabular diameter is 58 μ. The acetabulum is posterior to the middle of the body and, under pressure, or when the body is slightly extended, it is at the anterior edge of the posterior third of the body. It is 91 μ posterior to the oral sucker and 85 μ anterior to the posterior end. It does not project from the ventral side of the body.

Tiny papillae are on the ventral sides of both the oral sucker and acetabulum. These papillae are on the inner, ventral edges of the suckers close to the margins of their openings. A short distance posterior to the oral sucker is the pharynx into which a short prepharynx opens. It is of about the same length as the prepharynx, but slightly less in several cases, being only 20 μ long and 23 μ wide while the prepharynx is 23 μ long. Repeated attempts to see the digestive ceca in the living form were unsuccessful until neutral red was added to the water containing the cercariae. This makes them visible when great pressure is applied. About midway between the pharynx and the acetabulum the esophagus divides into two very narrow strands of tissue that represent the future functional crura. For almost their entire course these strands are solid and only in isolated places does a lumen appear. They extend posteriad to a point lateral to the midline of the acetabulum.

The stylet, as is usual, is inserted in the dorsal anterior lip of the oral sucker, and is moved about freely by the movements of the sucker's wall. The anterior third of the stylet is cone-shaped, with its point directed forward and its basal walls thicker than those of the anterior end, so that from a side view it appears to have a thickened hump or shoulder on either side of the base (Fig. 56). The posterior two-thirds is divided into two regions, an anterior part which constitutes by far the major portion of the stylet and which has reënforced walls of the same bluish material that is present in the walls of the cone, and a small posterior portion, darker in color, and solid in texture. It is definitely

separated from the anterior portion and lacks the thickened walls apparent in the rest of the stylet. The stylet is 30 μ long, with its pointed portion or cone not more than 7 μ in length.

A group of penetration glands lie lateral and anterior to the acetabulum, on either side of the body, the median glands of each group extending mesiad so that sometimes they meet in the region immediately anterior to the acetabulum. Repeated efforts to count the glands on each side gave varying results and led to confusion until it was finally determined with certainty that the same number of glands was not always present. This is interesting in that it is contrary to the condition in many other cercariae with regard to this character. It is often regarded as a character of great specific value in the identification of species but it is to be noted here that we must make allowance for this variation. Pressure enables one to see all of the glands clearly, each with its own nucleus, since they are all brought to the same level. Seven or eight glands are located on each side—only rarely are there six or nine—the median ones meeting in the midline.

A pair of ducts, two on each side and in close proximity, extend anteriad to the side of the stylet where they open to the exterior. The two ducts on each side twist about each other. This, together with the fact that they possess numerous swollen areas throughout their lengths, differentiates them from many other forms similar to *C. acanthocoela.*

Many small glands fill the body, both anterior and posterior to the acetabulum, each with a dark nucleus when in neutral red. A compact group of small cells lies between the oral sucker and the pharynx. Lateral bodies are thought to be cystogenous glands.

Two cell masses are present which are the early stages of the reproductive organs. One lies just posterior to the acetabulum and the other is just anterior to it. They are connected by a narrow strand of cells extending postero-laterad around the acetabulum.

Normally the excretory bladder, because of a constriction in its anterior region, consists of a posterior or caudal vesicle which opens anteriorly into a narrow lumen, and two lateral vesicles or arms with which this lumen connects. The walls of these arms, or bases of the main collecting tubules, are flexible so that they become periodically swollen with fluids (Fig. 54). This gives the appearance of three bladders in this cercaria, an important characteristic in identifying it if the functioning of the various parts is understood. The connections between these parts of the bladder are difficult to see when no pressure is applied (Fig. 57). Periodically the two lateral vesicles connect so that at this time there appears to be a single bladder, which extends horizontally. The fluids are then forced toward the center so that a median anterior vesicle

is formed, resembling greatly the above-mentioned caudal vesicle. The fluids are emptied posteriorly and fill up the caudal vesicle from which they are emptied to the outside through the excretory pore. This lies on the dorsal surface near the base of the tail, a short distance anterior to the posterior edge of the body. Under strong pressure the connections between these bladders all become widened so that the bladder is broad throughout its entire length and resembles a large Y. When the median part is sharply constricted the bladder appears to consist of an anterior V and a posterior rectangle. Thus the bladder assumes a great variety of shapes during its functioning and with varying degrees of pressure exerted by the cover-slip.

A main collecting tube extends anteriad from each arm of the bladder, and divides lateral to the acetabulum into a posterior and an anterior secondary tubule. The anterior tubule has four branches, and the posterior one two branches, each branch ending in three capillaries. Thus there are eighteen capillaries in each side of the body, twelve anterior and lateral to the acetabulum and six posterior to it. Of the anterior branches, one is lateral and slightly anterior to the acetabulum, one is lateral to the esophagus, one is lateral to the pharynx, and the fourth is immediately posterior to the oral sucker. The anterior branches of the two posterior ones are lateral to the median constriction of the bladder, and the posterior branch is in the extreme caudal portion of the body lateral to the setae pocket. Only four flame cells were identified but no doubt each capillary ends in one of these terminal cells.

The tail is usually contracted as it is pulled along by the animal. Since it has great powers of extension, large folds occur along its sides when contracted, but no fin-fold is present. When free from pressure, a lumen or core can be seen extending through the center. Scattered nuclei are present in the tail, an average of fourteen being there for four specimens studied. The width near the base of the tail is 36 μ. When contracted it is 0.117 mm. long and when mediumly extended it is 0.247 mm. long.

Nearly all of the liver tissue of the snail host had disappeared and the sporocysts were present in great tangled masses. These sporocysts are elongate, sac-like structures (Fig. 58) and vary a great deal in size and shape, depending on their age. The length varies from about 0.2 to 0.78 mm. and the width from 15 μ to 0.24 mm. The walls are thin and prolonged into knobs and swellings at various points. Cercariae, when mature, travel rapidly from one end of the sporocyst to the other and occasionally break through a tiny opening at one end of the sac which they have made by their own efforts. They squeeze slowly through

this opening and swim actively away. At least in the older stages these sporocysts have no power of independent movement.

Immature cercariae in a single sporocyst range from ten in number to one hundred and fifty.

In one large reddish-brown pigmented sporocyst a large quiescent cercaria was observed. It acted much as an encysted individual, had no stylet, was as large as, or larger than, the metacercaria of this form and resembled the metacercaria in anatomical respects, but had a small undersized tail which moved only slightly. This cercaria was nearly as wide as the sporocyst and appeared to be a giant individual among its fellows. Whether it represents a dual infection of the snail or a phenomenon as yet unexplained in the life history of *Cercaria acanthocoela* remains to be solved. I believe that this represents a cercaria that for some reason has failed to encyst.

Encysted individuals were taken from cysts in the liver tissue of the snail host (Fig. 59), but their scarcity indicates that in the majority of cases the cercariae do not return to encyst there.

When the transparent cyst wall was broken the worm moved about freely. The intestinal ceca are readily visible, reaching nearly to the posterior end of the acetabulum, and are noticeably wider and more developed than in the cercaria. No stylet was present but it was noticed in the wall of the cyst before the cyst was broken. The bladder is filled with granules and is truly Y-shaped. Spines are about evenly distributed over the entire surface of the body, and can be easily seen now. The body is about 0.280 mm. by 0.123 mm. and the distance between the oral sucker and the acetabulum is 61 μ. The acetabulum is 52 μ in diameter and 81 μ anterior to the posterior end of the body. The oral sucker is 69 μ wide and only 57 μ long.

Attempts to recover encysted individuals of this form from several species of fish, crayfish, and a number of frogs, were unsuccessful. However, cysts were found on *Notropis whipplii* Girard, sixteen hours after cercariae had been placed in the dish containing the fish. These cysts were fed to turtles, but with negative results.

C. acanthocoela differs from similar forms in several respects. It cannot be confused with *C. isocotylea* Cort 1914 because of the undeveloped digestive tract in *C. isocotylea* as shown by Cort (1914) and Faust (1918a). *C. polyadena* Cort 1914 has no esophagus or digestive ceca and has from ten to twelve penetration glands. *C. glandulosa* Faust 1917 differs radically from this form in the size of its stylet, the character of its excretory system, and the possession of numerous glands about its digestive tract. *C. diaphana* Faust 1917 differs from *C. acanthocoela* in the nature of its anterior glands, the proportions of its

two suckers, and the nature of its excretory system. Finally, *C. indica* XVII Sewell 1922 differs markedly from *C. acanthocoela* in regard to its excretory system, the size of its stylet, and its genital cell masses.

Cercaria tricystica E. L. Miller 1935

(Figs. 60-65)

This xiphidiocercaria was found in *Helisoma lantum* at Baton Rouge, Louisiana. Collections were made in June, 1932.

The body is bent ventrally and the tail lashes violently as the worm moves through the water. Soon the cercariae sink to the bottom of the container where they congregate in large numbers.

The body is flattened dorso-ventrally, much like that of *Cercaria mesotyphla,* and is oval in outline. When contracted or at rest the body is widest just anterior to the acetabulum. When at rest it is 0.224 mm. by 78 μ, when well extended 0.308 mm. by 56 μ and when contracted 0.196 mm. by 0.112 mm. The greatest width of the body when contracted is about 0.124 mm.

Spines are present at the anterior end of the body but they become smaller and more scattered posteriorly, until, posterior to the acetabulum, they cannot be seen.

The suckers are disproportionate in size, the oral sucker being larger than the acetabulum. It is about 52 μ in length and 59 μ in width when at rest, while the acetabulum is only 39 μ in diameter. The acetabulum is posterior to the middle of the body, being about 65 μ posterior to the oral sucker and 59 μ anterior to the posterior end of the body. It is located at the division of the median and posterior thirds of the body. The ventral sucker does not project ventrally as is common in many of these forms.

A short prepharynx and relatively large pharynx lead from the oral sucker. This pharynx is about 20 μ long and 20 μ wide. Posterior to it extends the narrow esophagus, which soon divides to form the equally narrow crura. They extend posteriad to about the horizontal diameter of the acetabulum (Fig. 60). These crura contain very narrow lumens, with numerous cell-masses, indicating that they are still undeveloped.

The mucin glands constitute a noticeable and distinctive feature of the cercaria (Fig. 61). Each lateral group is composed of nine glands which lie in the dorsal region of the body and lateral to the acetabulum. Each gland contains a large clear nucleus. All of the glands on each side connect anteriorly with a large lateral duct. In its posterior region this duct is bipartite but near the oral sucker each duct is composed of four separate parts (Fig. 60). Each duct opens at the side of the stylet, anterior to the walls of the oral sucker. Under pressure a sticky material passes out through the openings of these ducts.

The stylet is about 21 μ long and contains a dorsal ridge or swelling near the base of its anterior third (Fig. 62). A side view of the stylet indicates that this ridge does not extend ventrad (Fig. 63.)

A genital mass, which stains pink in neutral red, lies posterior to the acetabulum and extends to the right, passing forward along the right side of the acetabulum. It is composed of small spherical cells.

The excretory bladder varies in its shape because of pressure and contraction of the excretory pore. However, when not distended with fluid it often consists of three vesicles, because of a median constriction which separates the two lateral arms from the posterior vesicle. This constriction is weaker at times so that a broad T is formed. When the body extends this shape changes to a Y. The constriction is so minute that three separate bladders seem to be present. In this respect it resembles *C. acanthocoela.*

A main collecting tubule extends anteriad and laterad from each lateral vesicle and, lateral to the ventral sucker, divides into an anterior and a posterior secondary collecting tubule. The connections of the finer branches of this system have not been determined.

The tail is attached ventrally as noted above, and when the worm is not swimming the tail is contracted and has an irregular outline. It is much shorter than the body, being only 84 μ long when contracted and 34 μ wide at its base. When slightly extended it is 0.140 mm. long and when well extended it is 0.174 mm. long. Very narrow caudal pockets are present because of the above mentioned tail attachment but they are not readily seen. No setae are present in these pockets as is true of the pockets of *C. acanthocoela.* No caudal excretory tubule is visible but a narrow lumen is present in the tail which can be observed without the application of pressure. The tail has no fin-fold (Fig. 64).

C. tricystica develops in the liver tissue of *Helisoma lantum* which is crowded with very small oblong sporocysts, similar to those of *C. meniscadena.* In old infections I have never found more than one fully developed cercaria in a sporocyst (Fig. 65), but in the young forms several fully grown as well as numerous developing cercariae were found. The sporocysts possess transparent walls, but the walls of those containing active cercariae may contain a light golden-brown pigment. The wall is elastic and easily distorted by the cercariae within. It is thin and composed of large cells joined to each other in an irregular formation. Large individuals were 0.273 mm. long and 0.137 mm. wide but the averages for ten individuals were 0.195 mm. in length and 85 μ in width.

Cercaria tricystica differs from both *C. isocotylea* and *C. polyadena* in the relatively small size of its tail, the shape and size of its sporocysts,

the number of salivary glands, the possession of a complete digestive tract, and in several characteristics of less importance. It is unlike *C. diaphana* in that *C. diaphana* has caudal pockets lined with setae, a stylet nearly twice as large as that of *C. tricystica,* and eight penetration glands of much smaller size. The only other forms at all like *C. tricystica* are *C. glandulosa* and *C. indica* XVII. *C. glandulosa* contains numerous glands which line the digestive system; it also has pronounced caudal pockets which have spines as does *C. diaphana,* and it has a stylet larger than that of *C. tricystica. C. indica* XVII has pyriform salivary glands which differ in number and in the character of their ducts from those of *C. tricystica.*

Cercaria cystonchnoides E. L. Miller 1935

(Figs. 66-70)

Ampullaria depressa, collected at Leesburg, Florida, in October, 1931, was found to be infected with a very large stylet cercaria. The cercariae and sporocysts were present in the liver in immense numbers, such swarms of cercariae emerging that they soon made the bottom of the container white, when they began crawling about with their suckers. They continue their movements long after the tail has been lost. They remained alive in the containers for a period of thirty-six hours.

The body is elongate, bluntly rounded at its posterior end and drawn out to form a narrow projection at its anterior end (Fig. 68). A depression occurs at the posterior end of the body in which the tail is attached. The body is about 0.616 mm. long and 0.325 mm. wide when at rest. This width was taken through the acetabulum. The tail is about 0.504 mm. long when at rest. Thickly-set spines cover the entire body surface and are larger in the anterior region.

The large stylet is about 36 μ long and bears a swollen area, or ridge, at the base of its pointed anterior end (Fig. 67).

The tail, which has almost the same length as the body, has no excretory tubule, but its longitudinal core disappears when the tail is fully extended (Fig. 66). It possesses no fin-fold.

Numerous glands make obscure the excretory tubules in this form and many tiny globules are present through the entire body.

The penetration glands lie anterior to and on either side of the acetabulum, each lateral group consisting of a large number of glands so that I was not able to determine the number. The large penetration duct can be seen extending along either side of the body to its termination at the anterior end of the body near the base of the stylet. This termination is swollen, the enlargement being particularly noticeable when the worm is resting or is contracted.

The oral sucker occupies an antero-ventral position, being not quite subterminal. It is circular, being about 0.101 mm. in diameter. The acetabulum occupies a position very near the center of the longitudinal axis of the body but slightly posterior to it. It is unique in being slightly larger than the oral sucker, for it is about 0.104 mm. in diameter. The body extends 18 μ anterior to the oral sucker and 0.182 mm. posterior to the acetabulum. The ventral sucker is 74 μ posterior to the oral sucker.

The cavity of the oral sucker, opening posteriorly into a short prepharynx which is continued posteriorly into a muscular pharynx, measures about 0.299 mm. in length and 0.351 mm. in width when quiescent. The relatively short esophagus divides to form the intestinal crura which extend posteriad as narrow lateral tubes, reaching almost to the posterior end of the excretory bladder (Fig. 69).

The large excretory bladder opens through a dorsal pore to the exterior. It is rectangular when in a contracted condition, but when filled, it extends anteriorly as a large cone-shaped or pyriform vesicle, reaching to within a short distance from the acetabulum, where it divides into two antero-lateral siphons.

A mass of cells which probably represents the genital primordium lies posterior to the acetabulum.

Each siphon crosses the cecum and divides just anterior to the acetabulum, into an anterior and a posterior secondary tubule (Fig. 69). The posterior branch divides ultimately into three branches, each branch of which ends in three capillaries, each with its flame cell. The flame cells, which are constant in position, total thirty-six, eighteen on each side of the body. The anterior secondary tubule divides similarly into nine such collecting tubules. The anterior group of flame cells lies lateral to the oral sucker, prepharynx, and pharynx; the second group is in the immediate region of the union of the intestinal ceca; the third group is in the region between the second group and the acetabulum; the fourth group is lateral and posterior to the acetabulum; the fifth group is lateral to the excretory bladder; and the sixth group is lateral and posterior to the excretory bladder.

Upon opening this infected *Ampullaria depressa,* I found the liver to be bulging with thousands of cercariae and sporocysts in all stages of development. The excretory tubules and the bladder were not seen in the very young cercariae.

These sporocysts were quite heavily pigmented with a brownish-red pigment. Slight movement could be noted at the knob-like ends but the swollen portions, at least in the older individuals, exhibited none whatever. The majority of the sac-like sporocysts have two swollen areas filled with cercariae, and a neck-like constriction between them (Fig. 70). In many of the younger sporocysts only one of these swollen

areas is present. Matured cercariae are actively engaged in striking against the walls of the sporocysts with the stylet, and occasionally one escapes through the opening made in this wall. Germ balls in various stages of development are also present in large numbers.

This species represents one of the few forms ever described from Florida, and no Cercariae Armatae have ever been described which might be confused with it because of close similarity in structure. Its large acetabulum sets it apart from most other related forms. A few of these cercariae have been described which also have a larger ventral sucker than oral, such as *Cercaria tenuispina* Lühe 1909 and *Cercaria triloba* Filippi 1857, but confusion can be avoided because of other differences between these forms.

Cercaria steganocoela E. L. Miller 1935

(Figs. 71-73)

The host of this species of cercaria is *Physa gyrina hildrethiana* which was collected at Camp Creek near Seymour, East Lake Fork near Sadorus, and in the Drainage Ditch at Urbana. Material was obtained in April and May, 1932. Scarcity of material gave me no opportunity to make detailed studies of several features.

This form resembles *C. acanthocoela* and casual observation gives one the impression that it is *C. acanthocoela*. However, several differences will be mentioned.

It is an elongated stylet cercaria, having the jerky movement characteristic of these forms, as it swims through the water.

The body is narrower near its posterior end, and a little anterior to the posterior margin on the ventral surface of the body is the attachment of the tail. A deep groove on this surface into which the tail fits, gives rise on either side of the tail base to a deep caudal pocket which has its lateral wall lined with small spines, directed inward (Fig. 71).

Many spines are on the anterior end of the worm. They become smaller and are more scattered posteriorly until, in the region of the acetabulum, they are not visible.

The body and tail are of about the same length. With only little pressure the body is 0.224 mm. long and 0.168 mm. wide when contracted. When at rest both the body and tail are about 0.280 mm. in length, and the tail is 45 μ wide at its base. However, when well extended the body may be 0.460 mm. by 80 μ. The tail is pulled along as the cercaria crawls, beating vigorously when body movement occasionally ceases. A lumen is visible when the tail is not compressed. No fin-fold has been seen on the tail.

The penetration glands are peculiar in that in addition to a group of five to six glands on either side of the acetabulum, there are a few small

glands attached to the side of the ducts (Fig. 71). Two small glands are usually thus attached on each side but their position is so indistinct that it is impossible to determine their number with certainty. The large duct on each side of the body is twisted and swollen at intervals. It is narrower near the posterior border of the oral sucker, then swells and from here on to its anterior opening is tripartite. Just before opening to the exterior on either side of the stylet the ducts narrow rapidly and become very fine tubules, still, however, retaining a median striation. Droplets of a thick consistency form at the openings of these ducts when pressure is applied to the animal. Other small glands cover the body.

Small flattened masses of cells which represent the undeveloped genital system lie anterior and posterior to the acetabulum (Fig. 71).

The oral and ventral suckers are approximately of the same size. The length of the oral sucker averages 69 μ and its width 66 μ, while the ventral sucker is 67 μ by 65 μ. When the worm is at rest these two suckers are spherical. The acetabulum is in the center of the body, at a distance of 70 μ from the anterior end and 0.104 mm. from the posterior end of the body. It is 98 μ behind the oral sucker.

The stylet contains the characteristic thickening of cercariae armatae near the base of its anterior third (Fig. 72). This thickening does not extend ventrally as determined from side views. Near its base the thickened walls cease at a circular constriction and the stylet ends in a globular base which is enclosed in a thin wall and is composed of a homogeneous hyaline substance. The stylet averages about 27 μ in length but occasionally reaches a length of 30 μ.

Posterior to the oral sucker is a very short prepharynx which sometimes does not show. Posterior to it is the pharynx, an esophagus, and finally the two intestinal crura, which extend to within a short distance of the posterior end, almost to the back margin of the posterior excretory vesicle if the worm is not fully extended. These crura are very narrow and rudimentary and can seldom, if ever, be seen in the living animal unless it is stained with neutral red or a similar stain; then the worm must be subjected to great pressure. The tissue inside the walls of the crura stains deeply with neutral red and this material is seen to fill the lumen only at irregular intervals (Fig. 71). The development of this digestive system is an important difference between this form and *C. acanthocoela,* and constitutes one of the few useful characters in a separation of the two species.

The expulsion canal is composed of the following elements: a posterior rectangular vesicle which connects with its excretory pore by a narrow, short tube that opens at the base of the tail on its dorsal side; a median

anterior constriction which extends forward for a short distance before dividing to form a Y; and, finally, two lateral elongated vesicles posterior and lateral to the acetabulum which are really expanded portions of the basal ends of the main collecting tubules. These bladders often communicate with each other by forming a broad, transverse, single vesicle just before emptying into the posterior vesicle through the constricted anterior end of the median expulsion canal. Again, all three may be broadly joined so as to make a typical Y-shaped bladder. The bladder functions much as it does in *C. acanthocoela.* Main collecting tubules extend anteriad from these lateral bladders but the connections of the finer tubules and capillaries of the excretory system have not been determined.

Large, elongate, irregularly-shaped, yellowish sporocysts are found in the liver tissue of the host (Fig. 73). They are filled with many cercariae in different stages of development, from undifferentiated germ balls to mature cercariae seeking a way out of the sporocyst. Older infections were noted in which the liver seemed to be disintegrating even though the snail was still alive. In these snails the tissue was soft and broken but still filled with active cercariae. Many old, partially disintegrated sporocysts were found in these snails. It may be that when the cercaria is parasitic in several different species of snails, the more uncommon hosts are not able to withstand heavy infections, so that there is an actual disintegration of the liver, with the consequent death of the sporocysts. Disintegrating germ balls were also present. The average dimensions for ten of these sporocysts were a length of 4.5 mm. and a width of 0.252 mm.

While the digestive system of *C. steganocoela* is similar to that of about fourteen other species of these Cercariae Armatae, other differences such as the number of salivary glands on a side, the shape of the excretory bladder, the presence of large caudal glands, and the character of the genital masses enable me to differentiate it readily from these forms. I refer to such forms as the following: *C. stylobuccalis* Faust 1922, *C. microxiphifera* Faust 1926, *C. paracephaladena* Faust 1926, *C. cawstoni* Faust 1919, *C. ingracilis* Faust 1921, *C. humilis* Faust 1921, *C. cephaladena* Faust 1921, *C. tenuispina* Lühe 1909, *C. triloba* Filippi 1857, *C. limnaeae ovatae* v. Linstow 1884, *C. secunda* Sinitsin 1905, *C. dimorpha* Sinitsin 1911, and *C. cribrata* Sinitsin 1911. *C. candelabra* Faust 1919, the only North American form described up to this time which resembles *C. steganocoela* most in regard to the digestive system, differs from it in having an excretory bladder very different in shape, a smaller oral sucker, acetabulum and stylet, and in having a cluster of penetration glands on each side of the body with many in each cluster, while there are only from five to seven on a side in *C. steganocoela. C. pseudarmata*

Brown 1926 has only four penetration glands on each side, and *C. leptosoma* Brown 1926 has five.

It should be noted here that synonomy may be the result of earlier descriptions of forms in which no digestive system was seen beyond the pharynx, for improved methods have probably enabled workers to see structures which were not seen by earlier workers. This has been discussed earlier in this paper.

Cercaria pachycystata E. L. Miller 1935*

(Figs. 74-77)

Helisoma trivolvis collected at Camp Creek near Seymour, Illinois, in October, 1931, and at Mud Slough near Henry, Illinois, in June, 1932, was found to be infected with a small xiphidiocercaria belonging to the Cercariae Armatae. A detailed study in 1935 convinced me that this was a new species of cercaria.

Measurements were difficult to make on this worm since it was continually in motion, until the pressure of the cover-slip was great enough to distort the worm, or until stain such as neutral red or methylene blue had been added to the water. It crawls aimlessly about; the contracted tail is pulled along, and at intermittent periods it is extended and beats rapidly from side to side, as occurs commonly in the Cercariae Armatae.

The body is usually an elongate, flattened oval, but ribbon-like when well extended. The anterior end is narrower than the posterior end, which is broad and truncate. The posterior end is elevated dorsally so as to make a hump above the ventral attachment of the tail. The small acetabulum does not protrude ventrally. Many small oil-like droplets, bluish in color, are distributed through the body, and give this cercaria a distinctive appearance. Numerous small spines are on the anterior end of the worm, but they thin out posteriorly so that they do not reach beyond the acetabulum.

The length of the tail averages about one-half that of the body. The tail is inserted on the ventral side of the body a short distance from the posterior end. When it is contracted there is a dark area in its center with occasional droplets and groups of cells scattered through it. The tail has no fin-fold and no caudal excretory tubule. Few nuclei are present in the tail. The ratio of the body length to the tail varies with contraction. All width measurements were taken through the region of the acetabulum. With faint pressure the contracted body is 0.129 mm. by 0.168 mm. and when extended it is 0.392 mm. by 73 μ. Measurements

*Since the publication of the abstract of this monograph in 1935, the writer has found that *Cercaria tetradena* E. L. Miller 1935 is a homonym of *Cercaria tetradena* Faust 1924. References to this species elsewhere in the present paper have been changed to *C. pachycystata,* as the writer is here proposing the name *C. pachycystata* for *C. tetradena* E. L. Miller 1935.

taken to show the ratio of the tail and body length showed the quiescent body to be 0.336 mm. by 0.157 mm. when pressure was used. At the same time the tail is 0.169 mm. by 30 μ. These measurements show the tail length to be about half that of the body. The greatest length noted is that of 0.47 mm. for the body and 0.28 mm. for the tail when they were both fully extended.

The stylet has thick walls which become thinner in its pointed anterior cone; however, it lacks the pronounced swelling or ridge which is so common to those forms which we speak of as Cercariae Armatae. Its length averages 16 μ and its distal two-thirds consists of a hard, thickened outer covering, which comes to a point gradually (Fig. 76). It is in the dorsal lip of the oral sucker.

The oral sucker is located almost at the tip of the body. Prominent circular muscle fibers line the cavity of the sucker. The two suckers are equal in size, averages showing the diameter of the oral sucker to be 59 μ, that of the acetabulum to be 52 μ. Under medium pressure the acetabulum is about 0.13 mm. posterior to the oral sucker and 0.153 mm. anterior to the posterior end of the body. A long prepharynx, 30 μ long, a comparatively large pharynx, 23 μ by 34 μ, and a short esophagus are present. Near the acetabulum the esophagus divides into two narrow non-functional crura which extend posteriad almost to the end of the body and slightly posterior to the excretory sphincter (Fig. 74). Only by persistent pressure, staining, and use of oil immersion, can one see these in the living form.

Two large ducts extend posteriad from the anterior dorsal margin of the oral sucker and connect with a group of four large glands on each side of, and anterior to, the acetabulum. Each duct consists of three large strands clearly separated for some distance at their anterior end. Near the edge of the oral sucker the three strands unite or at least become twisted about each other, but finally widen again before they connect with the salivary glands. A group of closely-packed, very small cells or glands are also located along the ventro-posterior edge of the oral sucker.

The excretory bladder is unusually complicated. Just anterior to the union of the ventrally attached tail is a large sphincter possessing very thick walls and hair-like structures on its inner postero-lateral walls. It empties into a narrow canal which extends to the posterior end of the body above the tail base and opens to the exterior at the end of the body between it and the tail. Anterior to this sphincter extends a thick-walled canal, the posterior portion of which periodically expands into a bladder during the functioning of the expulsion canal. This canal is irregular in its course during contraction. Just posterior to the aceta-

bulum it expands into another transverse vesicle which is about as wide as the acetabulum (Fig. 77). The lateral portions of this vesicle pulsate, forcing liquid down the lumen into the posterior bulb of the bladder.

Each lateral bulb connects laterally with a main collecting tubule which, at its lateral extremity, divides into an anterior and a posterior secondary collecting tubule. Each secondary tubule has three branches, the anterior branch of the posterior tubule being directed forward while the posterior branch of the anterior tubule is extended posteriad (Fig. 77). Each branch, at least in the posterior half of the body, divides into five capillaries. However, the penetration glands and other material in the anterior half of the body make it difficult to determine the number of capillaries and flame cells there.

A single genital mass lies immediately posterior to the acetabulum and is composed of minute cells which stain pink in neutral red.

The mature sporocysts have walls containing much orange or brownish pigment, and they fill all available space in the liver of the snail (Fig. 75). They are elongate sacs with blunt ends and thin walls, and contain many cercariae in various stages of development. The sacs are not filiform in the sense of having a length at all comparable to that of the sporocysts of *C. mesotyphla.*

Various features of the excretory system, the salivary glands, genital mass, and digestive system of this species differ sufficiently from all described species to verify my statement that the above form is a new species. While *C. acanthocoela, C. tricystica, C. cystonchnoides,* and *C. steganocoela* bear certain features in common with *C. pachycystata* that suggest possible relationship, nevertheless *C. pachycystata* differs materially from those forms. Another form, *C. pseudarmata* Brown 1926, differs regarding its excretory bladder. *C. leptosoma* Brown 1926 has five penetration glands on each side. *C. pandora* Faust 1921 has four penetration glands on each side also, but its rudimentary intestinal ceca differ radically from those of *C. pachycystata.* (See footnote on page 72.)

Cercaria tridena nov. sp.

(Figs. 78-80)

Snails collected at Baton Rouge, Louisiana, in April, 1932, and later identified as *Helisoma lantum,* were found infected with a small xiphidiocercaria, whose structure has points in common with that of *C. steganocoela, C. tricystica,* and *C. acanthocoela.* However, its digestive system and salivary glands differ noticeably from those of the above cercariae.

The worm does not encyst after emerging from the snail but soon settles to the bottom of the container where it crawls about for approx-

imately twenty-four to thirty-six hours before dying. It is not a strong swimmer, but moves rather aimlessly through the water with its body contracted, and bent ventrally, while its tail lashes vigorously. The tail is short as compared to the body when the worm is at rest, and it contains lateral folds when contracted.

When the oval body is contracted the region just anterior to the acetabulum is much wider than the region posterior to this organ. Therefore, all width measurements were made in this region. The anterior end is often extended into a snout-like process when it is elongated, and at that time the length of the oral sucker is greater than its width.

When at rest the body is 0.196 mm. by 0.106 mm., but may vary from 0.168 mm. by 0.129 mm. to 0.392 mm. by 56 μ. The tail varies in size also. When almost completely contracted it is only 33 μ long and 73 μ wide at its base, but it varies from 0.112 by 0.14 mm. to 0.252 mm. by 26 μ. Thus the tail is slightly shorter than the body (Fig. 79).

Tiny spines, much smaller than those of *C. acanthocoela,* are in the anterior region, particularly lateral to the oral sucker. They thin out posteriorly and become much smaller, so that in the region of the acetabulum they are contained entirely within the cuticula. From a point a short distance back of the acetabulum to the posterior end of the body, no spines can be seen.

The caudal pockets are very much reduced so that the lumen is almost absent. Setae could not be found on the walls of these pockets.

When contracted, the tail is very short, being only a fraction of the length of the body. It is attached to the ventral side of the body, and a short distance in front of the posterior end of the body (Fig. 78). A narrow lumen extends through the tail, and ends distally in an enlargement a short distance in front of the distal end of the tail. This lumen possesses irregular swellings throughout its course. When the body is quiet or crawling along by means of its suckers, the tail beats much of the time.

The oral sucker is only slightly larger than the acetabulum. When slightly contracted it is 44 μ long and 93 μ in width while the acetabulum is 52 μ long and 56 μ wide. When at rest the oral sucker is 61 μ long and 72 μ wide. At the same time the acetabulum is 59 μ long and 59 μ wide. Thus the oral sucker is slightly the larger. It bears a comparatively small stylet which has the thickened ridge, or shoulder, at the base of its narrowed anterior third. However, this ridge is less pronounced than in the majority of these forms. Its thickened walls extend backwards on either side of the stylet, and end in the region of the murky base which is a small area definitely differentiated from the rest of the stylet by the absence of a thickened wall or hollow center. The stylet is

20 μ in length and 4 μ in width at its base. The acetabulum is about midway between the oral sucker and the posterior end of the body. It is 49 μ posterior to the oral sucker when the body is contracted and 0.104 mm. when extended. It is also 52 μ in front of the posterior end when contracted, and 0.117 mm. while the worm is extended.

Posterior to the oral sucker is a very short prepharynx which is evident only when the worm is extended (Fig. 78), a comparatively large pharynx measuring 23 μ in both length and width, an esophagus reaching about half-way to the acetabulum, and intestinal crura which lie close to the lateral margins of the acetabulum when the worm is contracted, but describe a broad arc when it is extended. They, as well as the esophagus, are very slender, and in various regions consist of solid masses of tissue. However, the posterior regions are, in all cases, hollow. These crura extend 52 μ posterior to the acetabulum, or for about half the distance between it and the posterior end of the body.

Ducts from the penetration glands pass forward to a point on either side of the anterior tip of the stylet and open to the exterior. Under pressure a thick liquid can be seen slowly exuding from these openings. Posteriorly the ducts possess many enlargements, apparently due to their twisting, and connect to the glands in the region anterior and lateral to the acetabulum. Only three large glands could be seen on either side of the acetabulum, with occasional lobes occurring in one or more of them.

Dark granular masses, of a murky gray color, extend along either side of the body from the posterior end to a point a little behind the oral sucker. These may be cystogenous glands. Other globular bodies are scattered over the body, most of them being anterior to the acetabulum. They are lighter in color than the penetration glands, and have definite clear walls. Genital cell masses lie immediately anterior and posterior to the acetabulum and consist of elongated masses of small spherical cells (Fig. 78).

The excretory bladder extends forward from the excretory pore almost to the acetabulum before dividing into lateral arms to form a broad Y. As it contracts this bladder may constrict at the anterior end of its stem; the fluids of the arms flow together, and there then appear to be two separate vesicles, a caudal and an anterior one. When the body is contracted these arms form an irregular transverse vesicle. However, I have never noticed the separated lateral bladders appearing as in *C. acanthocoela* and *C. tricystica*. A greatly twisted main collecting tubule divides lateral to the acetabulum and slightly behind it to form a posterior and an anterior secondary collecting tubule. Just anterior to the acetabulum the anterior tubule divides into two smaller branches, but due to the glandular nature of the body it is impossible to trace the tubules of the excretory system further.

The liver tissue of *Helisoma lantum* was literally replaced by an immense tangled mass of short, oblong sporocysts, with compact, smooth outlines (Fig. 80) rather than irregular ones as is characteristic of the sporocysts of many other Cercariae Armatae. Some older sporocysts are light gray in color but most of them are a brilliant orange. Many of these sporocysts contain encysted forms which will be described later. The sacs average 0.756 mm. in length and 0.14 mm. in width.

In one of these sporocysts a large overgrown cercaria was found much like the one found in the sporocyst of *C. acanthocoela.* This individual was tailless and had lost its stylet, but was filled with a great mass of material resembling cystogenous material which obscured most of the structures in the body. Its bladder was greatly swollen with excretory granules as is the bladder of the metacercariae, the digestive system was plainly visible with only slight pressure, and the worm moved slowly as does a metacercaria after being liberated from its cyst. This worm is 0.246 mm. long, when mediumly contracted, and 0.151 mm. wide. The oral sucker is 62 μ wide and 59 μ long while the acetabulum is only 49 μ long and 53 μ wide. The acetabulum is about 65 μ posterior to the oral sucker and 72 μ anterior to the posterior end. These measurements may mean that this individual indicates a dual infection but I do not believe the differences noted here warrant such a conclusion.

As previously mentioned, this form encysts readily within the sporocyst and liver tissue of the host. However, many never encyst, as shown by the fact that the encysted forms are present in relatively small numbers, in comparison with the immense number of cercariae that emerge.

The cyst wall is a clear, transparent, tough substance; and when the wall is broken, the worm begins to move about. Eight ducts open separately, dorsal to the cavity of the oral sucker. A group of tiny, elongated, tube-like structures was noted here in the cercaria before it encysted, but because of their minute size these structures could not be carefully studied. Distinct spines are on the anterior portion of the body, but become smaller posteriorly until, in the posterior region of the body, they cannot be seen. The excretory bladder is now a large sac-like structure filled with granules and the crura reach farther posteriorly than they did in the unencysted form. The lateral bodies, possibly vitelline follicles, present in the cercaria are now more pronounced, and many large cells with prominent nuclei are scattered through the body.

Another form, the cercaria of *Lissorchis fairporti* described by Magath (1917), resembles *C. tridena* superficially but cannot be mistaken for it because of the difference in the salivary glands and excretory bladder. The structure of its stylet is also different. *C. crenata* Faust 1917 differs from *C. tridena* in the number and arrangement of its

salivary glands, in the possession of two very unequal suckers, shorter digestive ceca, and various other characters of less importance. *C. leptosoma* Brown 1926 has five mucin glands on each side of its body.

IX. FURCOCERCOUS CERCARIAE

Discussion of the Group

The first furcocercous cercaria described was that one given the name *Vibrio malleus* by Müller in 1773. *Cercaria vivax* Sonsino 1892, one of the first to be described outside of Europe, was also one of the very earliest to receive a detailed description (Looss, 1896). Lühe (1909) briefly described the furcocercous larvae in Germany and neighboring countries but grouped two of these individuals with his Lophocercariae because they were monostomes. He described the furcocercous cercariae as follows:

> Distome Cercarien mit langem, an seinem freien Ende gegabelten Schwanze, in welchen der schlanke Körper nicht zurückgezogen werden kann. Entwickelung meist in sehr langgestreckten Sporocysten, welche (ob bei allen Arten?) selbständig beweglich sind, nur bei einer Art angeblich in Redien.

Lühe divided these forms on the basis of presence or absence of eye-spots. Lebour (1911) divided the British marine forms into two primary groups on the basis of development in sporocysts or rediae. Cort described the first form reported from North America, *Cercaria douthitti* Cort 1914.

Because of Leiper's work (1915) the schistosome cercariae were separated from other furcocercous forms by their lack of a pharynx, of pigmented eye-spots, and of a cuticular keel on the furcae, which are less than one-half as long as the tail stem. Cort (1917) divided several of these forms into three groups on the basis of presence or absence of pharynx and eye-spots but his scheme is too limited to allow the inclusion of all forms now known. Sewell (1922) gave the first complete survey of all furcocercous cercariae but he separated out all monostome forms since he considered the presence or absence of an acetabulum to be of prime importance here in a system of classification. However, McCoy (1928, 1929a) found that furcocercous monostomes may develop into adult distomes.

Faust (1924) divided these forms according to the excretory system's flame cell pattern because he believed it was a natural basis for such grouping. His belief that it is a common system carried over from the cercaria to the adult would seem to be refuted by Miller's statement (1926a) that flame cells of the cercaria might have potentialities for more rapid division such that the pattern of the adult worm could not be predicted. This has been illustrated in other forms, for instance, in the larval and adult *Schistosoma japonicum*.

Miller (1926a) in his comprehensive studies on furcocercous larvae divided all known forms into two main groups, the Apharyngeal Cercariae and the Pharyngeal Cercariae, which probably constitute natural groups. Each of these were subdivided according to whether the individuals were brevifurcate or longifurcate and distomes or monostomes.

The species included in my studies will be listed in their proper position in Miller's scheme of classification.

Apharyngeal Brevifurcate Distome Cercariae

Definition

All furcocercous cercariae with no pharynx, with furcae which are usually less than one-half the tail-stem length and frequently sharply delimited from the tail-stem and which have both a ventral and oral sucker were placed in this group by Miller (1926a). He defined the brevifurcate larvae as follows:

> Furcae usually less than one-half the tail-stem length; frequently sharply delimited from the tail-stem. Tail-stem diameter less than that of body; usually attached somewhat ventrally, sometimes decidedly so, such that a dorso-ventral mount is rare. Furcal fin-folds sometimes present. Body frequently very hyaline. Eye-spots may be present. Anterior organ a very highly modified oral sucker, with anterior thin-walled and posterior muscular portions; head gland usually present. Ventral sucker usually much smaller in diameter than anterior organ; very protrusible and often held protruded. Penetration glands very large; frequently divided into anterior coarsely granular and posterior finely granular cells. Penetration gland duct openings frequently capped by hollow piercing spines. Excretory openings at tips of furcae. Never more than one pair of flame cells in proximal part of tail-stem. Tail-stem wall usually provided with powerful longitudinal muscles. Caudal glands not conspicuous; when present, are not arranged in pairs along caudal excretory tube. Tail-stem and furcae usually spined; no sensory hairs. Furcae almost cylindrical in some larvae. Alimentary canal opens more or less ventrally as a capillary tube; ceca absent or at most very short.

Miller (1926a) divided the apharyngeal brevifurcate distomes into eight subgroups and designated them as Subgroup A, B, C, D, E, F, G, and H. He listed twenty-six such forms and I have found descriptions of additional ones, namely, *Cercaria syncytadena* Faust 1926 and *Cercaria anomala* Rao 1929.

Cercaria wardi Miller 1923

(Figs. 81-87)

During my studies of infected *Helisoma trivolvis* collected in an Oxbow north of St. Joseph in June, 1932, a unique furcocercous larva was discovered which was described and named by Miller in 1923, and later discussed in his monograph on the furcocercous cercariae. Additional information about this form may be of value.

The body is very thick so that usually it must be viewed from the side under the cover-slip, only rarely a dorsal or ventral view being obtainable. The body is humped above the tail insertion (Fig. 81) as is also that of *Cercaria gigas* Faust 1918. Spherical eye-spots are the most prominent features of the worm. Large prominent backward-pointing spines cover the anterior end of the worm, forming a thick crown over the front half of the swollen anterior portion of the oral sucker (Fig. 86) and reaching posteriorly for a distance of about 46 μ.

The body is broadly subquadrate at its posterior end, and narrowed anterior to the acetabulum. When the body is under medium pressure my measurements are as follows: Body length, 0.35 mm. and greatest width at the posterior end, 0.156 mm.; tail stem, 0.689 mm. long, 65 μ wide at base, 85 μ wide at its middle; furcae, 0.247 mm. long and 52 μ wide near base. These measurements slightly exceed Miller's.

The oral sucker is pyriform in shape (Fig. 86) with the posterior end smaller. It is about 0.13 mm. long by 68 μ in width at its anterior end and 39 μ at its posterior end. The acetabulum protrudes prominently and is easily everted by slight pressure. Its inside is thickly covered with small spines and the entire body contains tiny spines, those nearer the posterior end being embedded in the cuticula. The acetabulum is much smaller than the oral sucker, being only 50 μ in diameter. It is situated at the end of about the anterior two-thirds of the body. The esophagus extends ventrad and soon divides into the two intestinal crura which extend to the acetabulum (Fig. 81).

The circular eye-spots consist of spherical pigment granules which appear as a black mass in a cavity containing a transparent fluid. However, when these granules are scattered by pressure they are seen to be brownish in color. They are about 0.182 mm. posterior to the anterior end and 78 μ anterior to the acetabulum. Each measures 26 μ in transverse diameter and 20 μ in longitudinal diameter.

Many glands and other tissue fill the entire body of this cercaria. Penetration ducts, each consisting of several distinct parts, which open near the ventral border of the anterior margin of the oral sucker, emerge from the sucker ventrally and connect with a mass of five glands on each side of the body. They are clear in appearance and lie dorsal to the acetabulum in large part, immediately behind the intestinal crura. A large, irregular, granular mass lies just posterior to these glands and nearly fills the body space posterior to the acetabulum. This is the posterior mucin body formerly mentioned by Miller (1926a).

Just anterior to the posterior mucin gland, between it and the ventral sucker, is a germinal cell-mass. Surrounding the posterior mucin gland and particularly numerous dorsally, are many large gland-like cells, each with a large nucleus. These may be cystogenous in character. Authors

have used various designations for these bodies. The anterior region of the body is entirely obliterated after treatment with neutral red, because of these dark nuclei.

When quiescent the tail stem is twice as long as the body but it may be much longer than this when it is fully extended. The furcae, usually contracted, are a little shorter than the body. The stem is narrowed both distally and proximally and is attached to the ventro-posterior margin of the body. It is parallel with the longitudinal axis of the body. Muscle fibers are prominent and have been described by Miller (1923, 1926a). The furcae are slightly shorter than the body when quiescent under pressure but in this state they are always contracted so that the furcal fin-folds become fluted. Two dorso-ventral fin-folds extend along each furca throughout its length (Fig. 83) and possess numerous ray or rib-like structures, which are prominent at the end of the fin-fold (Fig. 82).

The study of the excretory system proved to be difficult since this system is obscured by the glands and other cells of the body. Two giant flame cells near the base of the tail stem constitute the most prominent feature of the tail. Measurements which include the basal or nucleated portion of the flame cells show it to be about 20 μ long while the flame itself is only 13 μ long. This vibratile portion becomes inactive when great pressure is applied and can then be studied in some detail. Even camera lucida drawings can be made during this stage (Fig. 87). The vibratile portion is clearly striated but there is no indication of there being separate cilia here. Four distinct dark bands, run longitudinally and three narrow, lighter striations separate them from each other. In motion this structure resembles the undulating movements of a vibratile membrane. The complete excretory system was determined (Fig. 84) and corresponds to the description given by Miller (1926a).

When the snail was dissected the liver tissue seemed to be a living mass of cercariae for the walls of the sporocysts are so thin, delicate, and transparent that they are very easily broken. I have never disentangled a complete sporocyst, but in a few cases have found parts of the sacs which contained maturing germ balls and cercariae (Fig. 85).

Miller placed this form in his Group E of apharyngeal brevifurcate distomes since all members of this group are unique in possessing a posterior mucin gland.

Cercaria pteractinota E. L. Miller 1935

(Figs. 88-93)

Specimens of *Physa gyrina* collected at Twin Lakes near Paris, Illinois, and at Baton Rouge, Louisiana, were found to be infected with a

large brevifurcate form; those of *Helisoma trivolvis,* collected at Camp Creek at Seymour, and at the Oxbow Lakes at Urbana and St. Joseph, were also infected with this cercaria. It hangs in the water with its head downward when not disturbed but can move rapidly forward by its tail movements. It has exceptional ability to extend itself, and the anterior end is sometimes drawn out to form a narrow neck, extending by an out-pushing process which is probably due to the ability of the anterior organ itself to extend. Under the cover-slip the long tail is a hindrance to locomotion by the suckers. The worm can live in tap water for a long time, having been observed in the water for a period of thirty-one hours, at the end of which several of the worms were still living.

The body is quite rectangular in shape, being wider at the posterior end than at the anterior, when even slightly contracted. It is long and comparatively narrow and may appear quite ribbon-like when completely extended (Fig. 92). The tail is nearly three times as long as the body when it is extended. The quiescent body is 0.27 mm. in length, and 0.363 mm. long when extended. The widest portion, just posterior to the eye-spots, is 0.104 mm. The tail stem is 0.532 mm. long and 56 μ wide, and the furcae are 0.185 mm. long and 28 μ wide at their bases.

An immense number of tiny spines covers the body but those over the anterior half of the oral sucker, or anterior organ, are much more prominent (Fig. 91). They are arranged in longitudinal and transverse rows but spaced so as to make diagonal rows as well.

The eye-spots are prominent features of the cercaria and are elongated transversely. They lie midway between the oral sucker and the small acetabulum. When the worm is at rest they lie 96 μ posterior to the anterior end, and when it is extended, about 0.156 mm. posterior, and 0.195 mm. from the posterior end. The two conspicuous black spots are large in comparison with the size of the body, being in width about one-third that of the body in that region. An eye-spot is about 39 μ in width and 12 μ in length. A small compact mass of pigment, which resembles the eye-spot of a planarian worm, lies in the center of each pigment mass. Two other prominent pigment masses are present, one on either side of the oral sucker near its posterior end. Other scattered brownish masses of pigment are distributed over the body, several of them being constant in position (Fig. 91).

When the worm is at rest, the distance from the base of the tail to its bifurcation may be nearly three times as great as the length of the body. A sharp division separates the tail stem from the furcae. These furcae bear fin-folds on both sides of the distal one-half to two-thirds of their length and each fold has numerous rays or ribs throughout its length (Fig. 90). A broad central lumen runs longitudinally through

the tail stem, extending also into the furcae, and is evident when little pressure is applied. The tail is inserted on the ventral side of the body and makes a noticeable angle with the long axis of the body because of this insertion. A membrane passes ventrally over the base of the tail, making a cup into which the tail fits. Longitudinal muscles run in a diagonal direction in the tail, both outer and deeper fibers being present. Two giant flame cells, very prominent, are in the basal portion of the tail stem.

The digestive system leads posteriad from the elongated oral sucker, no pharynx or prepharynx being present. The oral sucker is much larger than the ventral, measuring about 91 μ in length by 59 μ in width, while the diameter of the acetabulum is only 29 μ. The oral sucker is subterminal and fills the whole anterior tip of the body (Fig. 93). The small acetabulum is on the tip of a prominent knob and is circular, easily everted with pressure, has its inner surface covered with spines, and has a three-cornered opening. It lies 65 μ posterior to the oral sucker and about 0.124 mm. anterior to the posterior end of the body. The esophagus runs posteriad and ventrad but it could be traced in the living specimen for only a very short distance. It turns downward and runs ventrad to the two eye-spots, along the body wall.

Large ducts, tripartite in their anterior regions, pass posteriad over the oral sucker and extend ventral to the eye-spots, passing to a point slightly posterior to the acetabulum, where they communicate with the penetration glands. These glands fill a large portion of the body posterior to the acetabulum. They occupy the dorsal regions of the body, are granular, and distinguish themselves easily from the large lighter glandular bodies which fill most of the remaining space posterior to the eye-spots. However, under pressure these glands seem to fill the ventral regions posterior to the acetabulum.

Two or three ventral compact masses of dark cells lie posterior to the acetabulum in the ventral region of the body. Two medium-sized compact bodies also lie just above the acetabulum. These bodies probably represent the germinal masses of the cercaria. The anterior regions of the body are filled with tiny nuclei.

The excretory bladder is almost forked by an anterior mesial projection which incompletely divides it. The lateral main collecting tubules describe an elongated loop (Fig. 88) and then divide into anterior and posterior collecting tubules. A large median excretory tubule runs through the tail to its fork where the tubule also divides, one fork running into each of the furcae and extending to the very tip where it ends in a slight enlargement. Two giant flame cells are situated a short distance distal to the base of the tail, each connecting proximally with a tiny collecting tubule which runs through the base of the tail into the body.

The sporocyst of this form is a thin-walled, filiform sac. The walls of these sacs are so delicate that the separation of a single complete specimen from the tangled mass of the liver tissue of the host is extremely difficult. The walls are thin and easily broken so that it is not unusual to see the tail or body of an immature cercaria protruding through a break in the wall. The dark pigment granules sometimes give the walls a light grayish appearance but in most cases they are quite transparent. The sporocyst is so narrow that rarely more than a single cercaria lies lengthwise in the central cavity (Fig. 89). Several large cercariae and germ balls were found in the sacs in various stages of development. The powerful tail is usually coiled lengthwise in the sporocyst. The immature forms lack pigment except for the two large eye-spots posterior to the oral sucker.

Several of these forms were found encysted in the liver of the snails but in all cases the worm inside was dead. Undoubtedly this is not a normal procedure. Attempts to recover encysted forms of *C. pteractinota* from crayfish were not successful.

C. pteractinota belongs to Miller's group of apharyngeal brevifurcate distome cercariae. The relatively few penetration glands and the absence of eye-spots in all members of Group A prevents me from placing this form there, while Group B also is characterized by only a few of these glands, only five pairs. The small size and presence of a few penetration glands in members of Group C also separate them from this form. *C. pteractinota* lacks the posterior mucin gland of Group E, described above for *C. wardi.* The five distinct penetration glands and the posterior cell mass in members of Group G prevent me from listing *C. pteractinota* with these forms. *C. elephantis* Cort 1917 has a body and tail covered with spines and *C. echinocauda* O'Roke 1917 develops in rediae. *Cercaria gigas* Faust 1918 of Group H, has a much shorter tail stem, has flutings in the furcae instead of rays, has two distinct types of glands, lacks the pigment masses described for *C. pteractinota,* and has only a single germinal mass of cells. *C. pteractinota* must therefore be placed in Group F since it lacks the so-called posterior mucin gland and the head gland found in Group E. The possession of numerous pigment masses, of numerous penetration glands, of two germ masses instead of one, and of elongated sporocysts, instead of small oval ones, separates this new species from *Cercaria indica* XXXVI Sewell 1922, the only representative of Group F. More recent apharyngeal brevifurcate distomes such as *C. anomala* Rao 1929 and *C. syncytadena* Faust 1926 bear only a superficial resemblance to *C. pteractinota.*

Cercaria gigas Faust 1918

(Fig. 94)

This form was found only once in *Physa gyrina* collected in the Sangamon River near Mahomet, Illinois, on May 29, 1932. Formerly Faust (1918) reported this in *Helisoma trivolvis* and *Physa gyrina* from DeKalb, Mt. Morris, and Urbana, Illinois. Few additions to Faust's original description can be made since the snail host soon died after it was brought into the laboratory. The large, characteristic, pigmented eyespots lying at a point about one-third of the body length from the anterior end (Fig. 94), the absence of a pharynx, the presence of a small, spined, protruding acetabulum, the long tail stem with very short furcae, the snout-like, elongate oral sucker which is also covered with spines, the gland cells posterior to the acetabulum, and the large number of penetration glands all help to identify this form as the sole member of Group H of Miller's apharyngeal brevifurcate distome furcocercous cercariae.

Pharyngeal Longifurcate Monostome Cercariae

Definition

About one-half of the furcocercous forms possess pharyngeal sphincters. Miller (1926a) separated the longifurcate from the brevifurcate cercariae on the basis of the following description:

> Furcae longer than one-half the tail-stem, sometimes exceeding it; usually not sharply delimited. Tail-stem diameter approximately equal to that of body when fully extended; attached terminally, dorso-ventral mount the usual one. Furcal fin-folds absent. Body usually crowded with small parenchyme cells. Eye-spots usually absent. Anterior organ less highly modified; cells which possibly represent a head gland present in but a few larvae. Ventral sucker frequently large, in some cases of greater diameter than anterior organ. Penetration glands small in proportion to body; no differentiation into anterior and posterior sets. Usually coarsely granular, and acidophilic in sections. Solid piercing spines more frequent than hollow ones. Excretory openings typically mid-furcal. Usually two pairs of tail-stem flame cells, seldom confined to a strictly proximal location. Tail-stem wall frequently annulated; tail less powerful and more transparent. Conspicuous, more or less regularly paired caudal glands in a number of species. Tail-stem usually devoid of spines; furcae may be spined; sensory hairs on the tail-stems of several larvae. Furcae never cylindrical, usually much flattened. Alimentary canal usually opens terminally or subterminally; esophagus a fair-sized tube; ceca usually well-developed, frequently reaching almost to posterior end of body.

Miller also divided the pharyngeal longifurcate monostomes into three groups, the Vivax Group, the Tetis Group, and the Rhabdocaeca Group, and listed eight species as belonging to the three groups. Since then other forms have been described, namely, *Cercaria dorsocauda* Tubangui 1928, *Cercaria bessiae* Cort & Brooks 1928, and *Cercaria physae* Cort & Brooks 1928. The character of its excretory system indicates that *C. dorsocauda* undoubtedly belongs in the Vivax Group. *C.*

bessiae and *C. physae* belong to the Rhabdocaeca Group because they contain six posterior penetration glands instead of the numerous anterior ones characteristic of the Vivax and Tetis Groups. They also agree with other members of this group in possessing sensory hairs on the tail stem instead of spines, and in having an excretory system slightly different but still characteristic of the group.

The following forms have been placed in the Rhabdocaeca Group:

1. *Cercaria rhabdocaeca* Faust 1919
2. *C. hamata* Miller 1923
3. *C. multicellulata* Miller 1923
4. *C. dorsocauda* Tubangui 1928
5. *C. bessiae* Cort and Brooks 1928
6. *C. physae* Cort and Brooks 1928

Study of *C. hamata* and *C. multicellulata,* collected in Illinois, and of *C. bessiae,* collected in Louisiana, has been made. Also descriptions of two new species of these pharyngeal longifurcate monostomes will be given here, one species from Illinois and the other from Louisiana.

Cercaria hamata Miller 1923

(Figs. 95-98)

This cercaria was found in *Helisoma trivolvis* collected in the Oxbow Lakes near Urbana and St. Joseph, and in *P. gyrina hildrethiana* in Lake Decatur near Decatur, Illinois. Miller (1926a) reported it from the Urbana area. The worm lies in the water with its anterior end bent ventrally, giving the hook-shaped appearance characteristic of so many of these forms. Annulations appear as the worm contracts slightly but they are confined largely to the anterior one-half or three-fourths of the body surface. In locomotion the tail functions so that the cercaria swims backwards by jerky spasmodic movements.

Normally the stem and furcae are of about the same length, the body being slightly shorter. The width of the tail stem is equal to that of the body unless the body is greatly contracted. Under pressure the body is 0.224 mm. long, the tail stem 0.252 mm. long, and the furcae 0.235 mm. long. The body is 45 μ wide at its greatest width, the tail stem is 39 μ and the furcae 28 μ at their bases. However, average measurements for slightly extended specimens are: body 0.151 mm. long, tail stem 0.213 mm. long, and furcae 0.209 mm. long. Spines are present on the anterior tip of the body but do not extend much posterior to the region of the oral sucker.

An elongate, relatively large, terminal oral sucker empties into a very narrow, undeveloped prepharynx and tiny bulbular pharynx (Fig. 95). The anterior organ is not pyriform as it is in *C. multicellulata.* The short rhabdocoele gut represents the development of the digestive system beyond the pharynx. The oral sucker is 29 μ long and 33 μ wide when contracted and 39 μ by 23 μ when extended. No acetabulum is present but a circular mass of cells which separates the anterior pair of penetra-

tion glands from the two posterior pairs may be the undeveloped sucker. The pharynx is 12 μ in width and 9 μ in length while the prepharynx is about 12 μ long.

A group of six large clear nucleated penetration glands lies in the posterior region of the body. The three glands of each side are arranged in linear fashion and taper into the narrow ducts leading from each. When the body is contracted these glands become globular or even broadly rectangular with the transverse dimension greater than the longitudinal, but with body extension they become duct-like in appearance. A single clear vesicular nucleus is in the center of each gland. Each duct divides just in front of the anterior pair of glands, one duct passing to the anterior gland and the other dividing to connect with the two posterior glands (Fig. 95). Anteriorly the ducts continue to the oral sucker and pass through it, where they become greatly swollen and the two parts of the duct become distinctly separated. They open at the anterior end where they are associated with large, definitely pointed spines. For some distance posterior to the pharynx these ducts are indistinct in the network of glandular bodies and tissue there.

A mass of deeply-staining cells in neutral red, the germinal mass, is posterior to the penetration glands and anterior to the excretory bladder. Many small round nuclei are scattered over the body.

A small, constricted excretory bladder lies at the posterior end of the body; it is constricted near its middle so as to give the appearance of a double bladder. Extending posteriorly from this bladder is a single median tubule which runs along the longitudinal axis of the tail-stem and divides near the fork (Fig. 98). A small island of Cort is present. Each branch of this tubule extends through one-half the distance of the furca before ending in a solid rod of cells near its lateral border. I have never seen external openings for these tubules as described by Miller, but have seen a terminal solid mass there in some specimens. Anteriorly each of the main collecting tubules of the body divides into an anterior and posterior branch. The anterior ends in four capillaries, each with its flame cell, and the branches of the posterior end in six flame cells, four of which are in the body and two in the tail-stem (Fig. 95).

The tail-stem is attached terminally as in *C. multicellulata*. It bears numerous sensory hairs which number about fifteen or sixteen on each side (Fig. 96). Numerous caudal glands are present which become greatly flattened and distended under pressure. A wide, glandular lumen extends through this stem and divides to extend into the tips of the furcae. Many nuclei lie in the tail, both in the stem and furcae, and, from a surface view, are evenly distributed. Loose muscle bands extend throughout the length of the tail-stem and terminate in the furcae.

The furcae are very long, each as long as the tail-stem and longer

than the body when at rest (Fig. 98). No fin-fold is present. From four to six striations extend longitudinally through the furcae, the six distal striations decreasing in number near the basal region, until, at the proximal end, there are only four such lines. These striations do not occur in the tail-stem. They are easily seen in the living, unstained specimen after strong pressure has been used but cannot be seen in stained forms since the furcal nuclei obscure them. Two rod-like structures (Fig. 97) arise at the posterior border of the furcal union and pass through about half the length of the furcae before ending near the outer margin of the furcae in a tiny mass of solid tissue. Occasionally one of these passes to the inner margin instead of to the outer. Earlier in this study they were believed to be the furcal excretory tubules but their apparent permanence under pressure makes me believe they represent different structures.

Great masses of slender, thread-like parthenitae fill all available space within the outer membranes of the liver of the host. The sporocysts are attenuate structures and resemble a mass of slowly oscillating algae because of their power of independent movement. They can contract and extend and when contracted, swollen, bulb-like areas are present. They vary in color from orange to brown and contain developing larvae and loose tissue in their centers. Each is swollen at one end, and is unusually active in its movements, its tip contracting much as the anterior end of an adult trematode. These bodies vary greatly in size. Narrow portions of the sac are only 28 μ in width while the swollen active ends are 84 μ in width. The sporocyst averages about 56 μ in width and varies in length from 2.0 mm. to 9.73 mm. Many of the smaller ones are 3.5 mm. long. The birth pore mentioned by Miller was not observed.

C. hamata differs from *C. multicellulata* and *C. physae* in that it lacks the pigmented eye-spots which the latter forms have. *C. bessiae* has unpigmented eye-spots and also has no caudal bodies. No pharynx has been described for *C. multicellulata.* The possession of a well-developed digestive system, of a different excretory system, and of a radically different body outline differentiates *C. dorsocauda* from this form. *C. rhabdocaeca* lacks glands and sensory hairs on the tail-stem. Its bladder is very different from that of *C. hamata* and it has no island of Cort. The oval anterior organ, the tail-stem of uniform width, the limited body spines, the caudal bodies and sensory hairs, the island of Cort and body proportions all enable one to recognize *C. hamata.*

Cercaria multicellulata Miller 1923

(Fig. 99)

The *Physa gyrina hildrethiana* found to be infected with this cercaria

were collected at Seymour, Illinois, in Camp Creek, in April, 1932. Miller (1926a) reported it from Urbana, Illinois.

The cercaria hangs in the water with its furcae above and open. It may dash suddenly through the water with the furcae working so as to draw the body after them. The body is shorter than the tail-stem and the furcae, but not noticeably so. The tail-stem is slightly longer than the furcae when they are quiescent. Small, thickly-set spines cover the anterior end of the oral sucker but thin out rapidly posteriorly, reaching only to a point about midway between the anterior organ and the eye-spots. These small, pigmented eye-spots are about midway between the oral sucker and the posterior end of the body.

The tail is attached terminally and its stem and furcae are filled with many large nuclei. Caudal bodies or glands are also present in the stem (Fig. 99) and are much more easily seen in some individuals than in others, depending on the age of each particular cercaria. Small, narrow fin-folds extend along the sides of the furcae.

No trace of a pharynx or alimentary canal is evident. The large oral sucker is terminal and easily evertible, this action being repeated continually under observation.

The yellow, thread-like sporocysts were so tangled that individuals were not completely separated for study. Many parts of sporocysts were studied and found to be filled with germ balls and undeveloped cercariae in different stages of development.

The pyriform oral sucker, the extent of the spination, the two pigmented eye-spots, the uniform tail-stem, the thin furcal edges, the sensory hairs of the stem, the absence of a digestive canal or pharynx, the paired caudal bodies, the excretory system, and the mass of cells which separates the anterior pair of penetration glands from the two posterior pairs, which may be the rudimentary ventral sucker, all help to distinguish this form.

The absence of a pharynx separates this from other pharyngeal longifurcate monostomes. It also differs from all except *C. bessiae* and *C. physae* in the possession of eye-spots. Those of *C. bessiae* are not pigmented. *C. physae* has only five pairs of caudal bodies while *C. multicellulata* usually has about eight pairs.

Cercaria bessiae Cort & Brooks 1928

(Figs. 100-101)

The material which furnished the basis for the present study of this species was found at Baton Rouge, Louisiana, in April, 1932, in *Helisoma lantum*. Cort and Brooks have reported it from Douglas Lake, Michigan, from *Helisoma trivolvis*.

The cercaria hangs fairly motionless, head downward in the water for rather long intervals; then the furcae suddenly flip rapidly and the worm shoots upward in the water, the tail foremost. When at rest the body is characteristically bent downward like a hook, as mentioned by Cort and Brooks.

The body is elongated, with a round, narrow anterior end and subquadrate posterior end. Under slight pressure and when quiescent the body is no wider than the tail-stem. When at rest the body is usually slightly shorter than the tail-stem and furcae, while they are of about the same length. When neither extending nor contracting under the cover-slip the body measures 0.168 mm. by 40 μ, the tail-stem from 0.196 mm. to 0.241 mm. by 45 μ, and the furcae 0.185 mm. by 22 μ at their bases. When the body has the same width as that of the tail stem due to extension it is about 0.224 mm. long.

Under high power a group of thickly-set spines can be distinguished at the anterior tip of the body but they thin out rapidly posteriorly, not extending beyond the anterior third of the body. Annulations, due to the contraction of circular muscles, are present on the anterior portion of the body. Two unpigmented eye-spots are located just anterior to the first pair of penetration glands (Fig. 100).

The tail-stem has a nuclear core which extends through its longitudinal axis and also into the furcae. This stem is inserted in the body terminally, it lacks caudal bodies but has from six to ten sensory hairs on each side. Surface nuclei are also present in the stem, and a single focus indicates that they are distributed regularly along either side of the stem, and through most of the furcae. Fine striations extend from the bases to the tips of the furcae of the tail; six rows or lines commonly are present.

The oval anterior organ is 33 μ by 20 μ; it is followed by a short prepharynx, a small bulbular pharynx about 10 μ long, and a short rhabdocoele intestine. A group of minute cells which separates the two anterior penetration glands from the four posterior, is interpreted as the rudimentary acetabulum.

The genital primordium at the posterior end of the body just anterior to the excretory bladder consists of a large mass of compact, deeply-staining cells in neutral red.

The two penetration ducts open at the anterior end in close association with the numerous spines mentioned previously. Each duct is bipartite, is swollen in its course through the anterior organ, and extends posteriad to connect with the penetration glands. Near the posterior edge of the oral sucker these ducts decrease noticeably in size, but increase in their posterior regions again where they lie close together, near the median plane of the body, when the worm is not subjected to pressure. When

pressure is applied they are pressed some distance apart and define a wavy regular course. There are three penetration glands on each side in the posterior region of the body. One-half of each mucin duct connects with two posterior glands, running under the anterior gland, while the other half of the duct connects with the anterior gland. The large, clear nuclei are numerous in the body of the living worm.

The bladder has a lateral constriction so that it is partially divided into a small posterior and a large anterior part. Lateral collecting tubules divide to form a posterior and an anterior secondary tubule near the anterior penetration gland and branch in the manner described by Cort and Brooks (1928). I have not succeeded in determining the connections of the third pair of flame cells because of the parenchyma which obscures this region.

Cort and Brooks did not describe the sporocyst of this form. The liver tissue of *Helisoma lantum* is filled with very long, narrow parthenitae (Fig. 101) which occupy all available space. Few developing forms are in the central cavities but granular material is profuse. Brown and orange pigments give these sacs their characteristic color, which is of a deeper brown in the swollen parts of the sac. The ends are swollen and the outline of the entire sporocyst is irregular, due to swollen areas alternating with constricted neck-like regions. It is very difficult to remove a single complete sporocyst from the tangled mass in the liver of the host. The narrowest width observed in the sporocyst was 28 μ, the average width was about 56 μ, and the width of the swollen end was 0.112 mm. The largest forms are 5.6 mm. in length.

This is the only species of the pharyngeal longifurcate monostome forms which has unpigmented eye-spots. Other differences between these species which prove to be of value in separating *C. bessiae* are: The possession of caudal bodies by *C. hamata, C. multicellulata,* and *C. physae;* the spines over all the body and tail of *C. dorsocauda;* the absence of a pharynx in *C. multicellulata;* and the different excretory system and large island of Cort in *C. rhabdocaeca.*

Cercaria furcalineata nov. sp.

(Figs. 102-104)

Helisoma lantum collected at Baton Rouge, Louisiana, in April, 1932, were found to be infected with a pharyngeal longifurcate monostome cercaria different from all those of this group previously described.

It hangs in the water in a manner similar to that described for *C. bessiae,* and its anterior end is bent downward to form a characteristic hook (Fig. 103). Its method of locomotion is similar to that of *C. bessiae.*

The body is not greater in width than the tail-stem when at rest or extended. When at rest the body is about 0.168 mm. long by 39 μ through its greatest width, the tail stem is 0.28 mm. long and 39 μ wide, and the furcae are 0.252 mm. long and 22 μ wide at their bases. When contracted the body is 0.101 mm. long and 56 μ wide. Under strong pressure with the body only slightly contracted it is 0.111 mm. by 72 μ, the tail stem is 0.247 mm. by 42 μ, and the furcae are 0.247 mm. by 26 μ. These measurements indicate that the body is shorter than the tail-stem or the furcae, and that the stem and furcae are of about the same length.

Spines are present at the anterior end but were not seen in the regions posterior to the oral sucker.

The tail is attached to the ventro-posterior tip of the body. The stem and furcae contain a great number of scattered nuclei which are most abundant in the lumen and along their sides. Five or six striations extend lengthwise through the furcae and resemble those which I have previously described for other pharyngeal longifurcate monostomes (Fig. 104). These broken lines have not been mentioned by other workers. I know of no function which they might perform except possibly that of giving rigidity to the furcae. They do not extend above the base of the furcae. A single, broken, linear-like rod extends outward from each side of the furcal union and ends near the outer wall of the furca. The terminations vary in different individuals and may be occasionally on the inner wall of the furcae (Fig. 103). Possibly these rods also give rigidity to the furcae. They differ from those described for *C. hamata* which were continuous. Several pairs of large, elongated, irregular bodies lie in the tail-stem on either side of the central excretory tubule which runs along the dorsal side of the tail-stem. Ordinarily two pairs of these glands are readily seen but in a few cases a third pair was noticed which was nearer the base of the stem. The sides of the stem are thrown into tiny irregular folds when the tail is slightly contracted, due to the circular muscle fibers in this region. Bundles of longitudinal fibers extend through the stem and into the furcae.

The oral sucker is elongated and oval in shape and measures 26 μ in length by 16 μ in width. Its narrow cavity opens into a short prepharynx which connects with a small bulbular pharynx. No other part of the digestive tract was observed.

A group of six penetration glands lies in the posterior half of the body but further anterior to the bladder than those of *C. hamata* and *C. multicellulata*. These glands are smaller and more easily broken under pressure than those of *C. bessiae* and similar forms, and cannot be detected easily even with the use of neutral red, since the entire body is literally packed with tiny, irregular or spherical nuclei which obscure all

structures in the body. Only the regions immediately lateral and posterior to the oral sucker are free from these nuclei. They make it very difficult to study the penetration glands and to determine their connections with their ducts. The glands differ from those of related forms in that those of a pair are usually not directly opposite but may be shifted anteriorly or posteriorly from such a position (Fig. 102). The ducts are bipartite and define a wavy course to the oral sucker. They narrow noticeably just before entering this organ, then swell to several times that of the posterior diameter. Each duct finally separates into two distinct parts just before opening at the anterior end of the worm in the region of a group of long spines.

A genital mass of small cells is just posterior to the penetration glands. When the bladder has emptied, two large globular cells can be seen in the posterior end of the body. Each contains a very large vesicular nucleus. Their function is unknown. No primordium of the acetabulum is evident.

The small excretory bladder has a lateral constriction which divides it into anterior and posterior parts. A caudal tubule extends along the median dorsal side of the tail and ends at a point exactly between the two furcae at the posterior margin. No branches have ever been seen in the furcae of the tail. The excretory pore opens on the dorsal side near the posterior end of the animal. The bladder gives rise to two main collecting tubules, each of which divides lateral to the anterior penetration glands. A posterior branch extends into the tail but flame cells were not seen in the stem. The anterior collecting tubule soon divides into two, the median one soon dividing again into two, an outer and an inner branch. The inner branch redivides and its mesial branch extends across the body and meets that from the opposite side to form a broad connecting loop just anterior to the mucin glands. The excretory system of this form differs in this respect from other members of this group but I am certain of the existence of this loop even though the terminal capillaries and cells of the excretory system were not traced.

This cercaria differs from all other described pharyngeal longifurcate monostomes in its possession of mucin glands of very indistinct character, small size, and uncertain position; an excretory system with at least one large anastomosing loop; the presence of two large globular cells near its posterior border; very numerous, closely packed body nuclei; and the existence near its furcal union of two discontinuous or broken rod-like structures differing from the solid ones of *C. hamata.* It also lacks the eye-spots of *C. physae, C. bessiae,* and *C. multicellulata,* the numerous body and tail spines of *C. dorsocauda,* the larger penetration glands of *C. hamata,* and the island of Cort of *C. rhabdocacca.*

Apharyngeal Longifurcate Monostome Cercariae

Definition of the Group

A discussion of the apharyngeal brevifurcate distomes has been given previously. Those of the present group differ in having the furcae longer than one-half the tail-stem length, and in other features mentioned in Miller's description of the longifurcate forms. These forms have no ventral sucker.

Miller (1926a) found only one such form described in the literature up to that time, namely *Cercaria indica* XXVII Sewell 1922. One other form has more recently been described, *C. sewelli* Faust 1926.

During the present studies a member of this subgroup was found in *Physa gyrina* which was collected at Baton Rouge, Louisiana, in 1932. Morphological studies on this form enabled me to designate it as a new species in an earlier paper.

Cercaria louisiana E. L. Miller 1935

(Figs. 105-108)

Physa gyrina collected near Baton Rouge, Louisiana, in June, 1932, harbored an apharyngeal longifurcate monostome which I have designated as *Cercaria louisiana*. The worm is very active in the water, and when in contact with a substratum, turns its ventral side downward (Fig. 108). For this reason it is nearly always observed under the microscope with its dorsal side uppermost. The body contracts and extends slowly but the tail-stem has less power to do so. The hook shape, seen from side view and mentioned for many pharyngeal longifurcate monostomes, was not noticed for this form.

When well extended the body is as narrow as the tail-stem, with the exception of the very posterior end. The anterior end is bluntly rounded and bears on its surface a crown of large, narrow spines seen easily under low power. They reach posteriad for not quite one-third of the length of the oral sucker (Fig. 105). As the worm contracts large annulations appear which reach posteriad for about two-thirds of the body's length.

The body normally is a little shorter than the tail-stem, and the tail-stem and furcae are of about the same length. Under slight pressure the body is 0.168 mm. long, the tail-stem 0.224 mm., and the furcae 0.224 mm. At the same time the body is 43 μ wide, the tail-stem is 33 μ, and the furcae are 17 μ at their base. The stem does not taper at its distal end. Under great pressure the body is 0.196 mm. long but the tail-stem and furcae still measure 0.224 mm. in length. The body of the worm is slightly prolonged ventrally and this projection fits into the

tail's attachment (Fig. 105). A dorsal projection of the body covers the tail's attachment.

No caudal bodies are in the tail-stem. However, many nuclei are in both the stem and furcae (Fig. 106), and extending through the center of the tail is a broad band of muscle fibers. The band splits into two parts at the distal end of the stem and each part passes into a furca, reaching to its distal extremity. Also a horizontal band of fibers connects one furca with the other and fuses with the other band in each furca (Fig. 107). A narrow fin-fold is present on each furca. The delicate striations so commonly observed in the furcae of the pharyngeal forms are also present in this form, but the lines are less distinct, being more broken and fused than in other forms.

The terminal opening of the anterior organ opens into a narrow cavity lying between the swollen penetration ducts and extending through the sucker. No other part of the digestive tract was observed. The large, elongated, oval, oral sucker is about 59 μ long and 29 μ wide. No acetabulum is present but a packed group of small cells which lies between and slightly posterior to the two anterior penetration glands may represent the undeveloped ventral sucker.

Two dorsal, pigmented eye-spots are just in front of the anterior penetration glands. Each is a small, circular, compact body but pressure causes it to separate into a number of pigment masses. The eye-spots are ventral to the penetration ducts.

Six large penetration glands lie in the posterior region of the body, the anterior pair being just behind the small eye-spots. Their ducts extend forward as bipartite structures, the median half of each duct being filled with coarser granular material than that of the outer part of the duct. In the region of the oral sucker the ducts become very voluminous but narrow again just before opening on either side of the mouth opening near the dorsal side of the body. The inner part of each duct connects with an anterior gland while the outer part divides into two ducts each connecting with one of the two posterior glands.

Posterior to the penetration glands is a large mass of cells, the germinal primordium. Many deeply-staining nuclei cover the body's structures as they do the stem and furcae, but they are particularly dense in some regions of the body.

The lateral constrictions of the small excretory bladder are not pronounced. The excretory system was not studied further because the hosts did not live long enough to enable me to do so.

C. louisiana differs from *C. indica* XXVII in lacking the rhabdocoele gut and the numerous penetration glands of *C. indica* XXVII. Also the eye-spots of *C. indica* XXVII are non-pigmented, and its furcae are without the folds described for *C. louisiana*. *C. sewelli* differs from the above species in possessing a dorsal body keel, eye-spots with pigmented

centers and only two pairs of penetration glands. Both *C. furcalineata* and *C. bessiae* differ from *C. louisiana* in lacking the furcal fin-folds which it has.

X. CERCARIAEA

History and Definition

This name was first used by Diesing (1855) as a collective group name and not as a true generic name, for a group of little known larval trematode forms. Lühe (1909) defined the group as "Distomenlarven, bei welchen die Ausbildung eines Schwanzes überhaupt unterbleibt," and separated it into the two larval genera Cercariaeum s. str., and Leucochloridium.

Carus (1835) created the genus Leucochloridium to contain a species of larval trematode which he named *Leucochloridium paradoxum,* which Zeller found later developed into the adult *Distomum macrostomum.*

Since Carus' description of the first Leucochloridium from *Succinea amphibia* on an island in the Elbe, several of these larval forms have been described. However, Leucochloridium larvae have probably been discovered three times in North America up to this time. Call (1898) in speaking of *Succinea obliqua* in Indiana said, "the tentacles are rather large and thick, club-shaped, and are often the home of a stage in the development of a planarian." Ward (1918) states that Bryant Walker, in a personal letter, reported finding the larval stage of a Leucochloridium in *Succinea ovalis* in Michigan. Magath (1920) reported a larval form from Fairport, Iowa, and gave it the name *Leucochloridium problematicum.* He reported it from both *Succinea retusa* and *Planorbis trivolvis. L. assamense* was reported by Sewell (1922) from India, and *L. millsi* by Faust (1924) from China. *L. cercatus* has also been described by Monticelli.

The recent discovery by McIntosh (1927, 1932), in Michigan, of adult Leucochloridium has added significance in connection with the following second detailed report of the larval form from North America.

Leucochloridium problematicum Magath 1920

(Figs. 16-19)

On October 8, 1931, I collected two *Succinea ovalis* Say from smart weeds, above the water at Cole's Pond, Charleston, Illinois, and upon opening one of them I found a large capsule-like object in one of the tentacles which proved to be the large branch of a sporocyst inside the body of the snail. The proximal end is very narrow while the distal half

of the sporocyst is banded with deep golden or brownish-red bands, varying in hue from almost yellow to brown and reddish-brown.

This larva is remarkably like the one described by Magath (1920) at Fairport, Iowa, and which he called *Leucochloridium problematicum.* This larva also resembles the one first described by Carus (1835) which he named *L. paradoxum.* Of course the possibility arises that perhaps the green-banded sporocyst of Carus and the brown-banded ones which Magath and I have reported are one and the same larva. Later work may throw light on this subject. This sporocyst is about 12 mm. long in the living condition and tapers into a thin thread at its proximal end, while the distal end is narrowly rounded (Fig. 17). The wall of the sporocyst is very tough.

Small larvae could be seen inside the body. It is circled by reddish-brown bands at its distal end, there being four of them. Proximally the bands grow lighter, fading to a yellowish color, until, about midway between the two ends, two broad, reddish-brown bands again occur, being perhaps more brownish in color than the distal ones. Faint yellowish spots were also noted near the proximal end of the sporocyst. The color varies somewhat from that shown by Magath (1920) for *L. problematicum;* also the size is greater. However, it is very likely that his measurements were taken from preserved specimens while mine were made from the living worm. Nevertheless, the preserved sporocyst measured 6.0 mm. in length, which is still greater than Magath's measurements.

This sporocyst contained 147 small larvae, each enclosed in a relatively large, two-layered, transparent sac (Fig. 18), with the two suckers separated from the rest of the sac at their openings by a bulb-like, thin, transparent membrane (Fig. 19). The larvae twist about in their sacs, and in doing so they move the sacs about as though they were parts of the larvae's bodies. These sacs are about 1.37 mm. in length and about 0.823 mm. in width through their acetabular regions. The measurements were made from living worms without subjecting them to pressure. Some cysts are elongated and of a brownish color, some smaller and round and of a clear transparent color. The sporocyst was opened at 9:30 p.m. on the 13th of October and the larvae within were placed in salt solution. All of the cysts had partly dissolved by 11:00 a.m. on the 14th. The cysts about the worms which I fixed in warm Gilson's fluid also disintegrated.

The larvae are oval in shape, rounded at the anterior and narrower at the posterior end. When well extended they measure about 1.206 mm. in length and when contracted, about 0.767 mm. in length and 0.514 mm. in greatest width, taken through the region between the pharynx and acetabulum.

The oral sucker and acetabulum are large in proportion to the size of this tiny worm, the acetabulum lying near the anterior margin of the posterior third of the body. However, in the preserved specimen this is somewhat different, with the acetabulum at the anterior half of the body, as described by Magath. The suckers are both powerful, more so than they are pictured by Magath. The oral sucker is 0.297 mm. in length and 0.322 mm. in width when contracted, and about 0.3 mm. in length and 0.2 mm. in width when extended. It is situated about 56 μ posterior to the anterior end of the body when the body is extended. A very brief esophagus is evident when the worm is greatly extended; however, in the contracted, preserved individuals this cannot be seen. The pharynx in the living specimen is only slightly wider than long but in the preserved specimen measures 57 μ long and 0.124 mm. wide. In the living animal it is about 0.15 mm. long and 0.10 mm. wide when the body is extended. There is no prepharynx.

The two intestinal crura extend, in a wide arc, almost to the posterior end of the body (Fig. 16). In a contracted or preserved specimen they define a broad curve as they extend posteriad. The distance from the acetabulum to the posterior extremity of the body is about 0.277 mm. The large acetabulum is 0.24 mm. in diameter. It lies about 0.25 mm. back of the posterior end of the oral sucker, its anterior margin not reaching to the middle of the body. As mentioned previously, this position is greatly altered by preservation. The posterior ends of the ceca are slightly pointed and the thickened walls extend throughout their length.

The excretory bladder is relatively very small in proportion to the size of the worm and lies close to the posterior extremity of the body. It extends diagonally in a postero-dorsal direction where it opens through the excretory pore which is close to the posterior extremity of the body. Two powerful siphons extend anteriad, and lateral to the ceca to a point lateral to the oral sucker, then turn posteriad and at a point just anterior to the bladder divide into several secondary branches. The largest branch extends anteriad, giving off branches in its course, until it ends as a single fine collecting tubule lateral to the oral sucker. Each capillary ends in a flame cell but because of the intricate network of vessels and flame cells (Fig. 16) it was impossible to be certain of the connections of all parts of this complicated excretory system. Material on hand was limited.

The genital organs are well developed in these larvae; the two testes, the ovary, the rounded organ, and cirrus sac that Magath (1920) mentions for *L. problematicum* are all readily identified. The genital opening is on the dorsal side of the body and posterior to the reproductive organs. It is near the posterior extremity of the body, even posterior to the excretory pore.

The locations of these reproductive glands vary in the preserved and mounted specimens. It should be noted that the testes are described here as elongate ovals rather than spheres, as they have been pictured in drawings of *L. problematicum* and *L. paradoxum*. Measurements of these organs in preserved specimens were taken. The anterior testis is to the right of the midline and is 67 μ long; the left posterior testis is 57 μ long; the spherical ovary is on the left side of the body and is 52 μ long and 48 μ wide; the elongated cirrus sac tapers anteriorly and is 76 μ by 48 μ; the so-called round body, lies between the two testes, and it is 48 μ in diameter.

In spite of several differences between these forms under discussion, I shall not designate this form as a new species, since work is being continued regarding its life history and morphology. With the present evidence, I am inclined to refer to it as only the first report of *Leucochloridium problematicum* from Illinois, and the second report from North America.

XI. SUMMARY

1. The larval trematode fauna of areas of Illinois, Louisiana, and Florida has been studied.

2. Nineteen previously described species from Illinois, Iowa, Michigan, Louisiana, Florida, and Wisconsin have been studied.

3. Four new species have been added to the list of North American forms, one from Florida, two from Louisiana, and one from both Illinois and Louisiana.

4. All descriptions were made from the living animal under uniform conditions.

5. Each species has been placed in its proper group, the history and definitions for each group having been previously given.

6. The twenty-three larvae are one Cercariaeum, two Gorgoderines, one Monostome, one Echinostome, one Cercaria Ornata, three Cercariae Microcotylae, six Cercariae Armatae, three Apharyngeal Brevifurcate Distome Furcocercous Cercariae, four Pharyngeal Longifurcate Distome Furcocercous Cercariae, and one Apharyngeal Longifurcate Monostome Furcocercous Cercaria.

7. Several new hosts and many new localities were found for previously described cercariae.

8. Complete infection records for all forms have been correlated in tables.

9. An identification key for all described Illinois larval trematodes has been prepared.

10. The relative merits of various morphological features of the larva for diagnostic value have been discussed.

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EXPLANATION OF PLATES

Unless otherwise stated, all drawings were made from living material under pressure of the cover-slip, with the aid of a camera lucida. Outlines, and in most cases, the suckers, were drawn with camera lucida and the remaining structures inserted free-hand. In all cases the penetration glands were drawn after neutral red had been added.

Abbreviations

a anterior (penetration) organ
ac anterior cell mass
av anterior vesicle
b folded body
bp birth pore
c covering cells of bladder
ca capillary
cb caudal body
cc cyst cavity
cg cystogenous gland
cl caudal lumen
cn caudal nucleus
cp constriction
cpo caudal pocket
cs cirrus sac
ct globe cavity
d duct of penetration glands
e encysted individual
eb excretory bladder
eg excretory granules
f fin-fold
fr furcal rays
fro furcal rod
fs furcal striations
g gelatinous cyst
gb germ ball
gc germ cell-mass
i island of Cort
l longitudinal muscles
lv lateral vesicle
mc main collecting tubule
me median eye-spot
o ovary
pe pigmented eye-spot
pg penetration gland
pl posterior locomotor appendage
pm posterior mucin body
pv posterior vesicle
rb round body
s swollen ridge
sc secondary collecting tubule
sh sensory hairs
sm sphincter muscle
t testis
tf tail folds
tg tail globe
tt thread of tail
vc vesicular cell

PLATE I

Note.—Fig. 8 is semi-diagrammatic; the scale for Fig. 6 represents 0.01 mm.; scales for Figs. 1, 2, 5, 13, and 14 represent 0.05 mm.; scales for all other figures represent 0.1 mm.

FIGS. 1-9.—*Cercaria sphaerocerca*

FIG. 1.—Ventral view, digestive system shown in broken lines to denote position in body; suckers semi-diagrammatic.
FIG. 2.—Structure of tail globe under pressure.
FIG. 3.—Encysted worm in proximal cavity of tail globe.
FIG. 4.—Entire tail appendage showing three distinct parts.
FIG. 5.—Side view showing prominence of ventral sucker.
FIG. 6.—Side view of stylet showing its dorsal hump.
FIG. 7.—Distribution of nuclei in distal portion of tail as revealed by neutral red.
FIG. 8.—Various shapes assumed by the bladder during life; semi-diagrammatic.
FIG. 9.—Sporocyst showing undeveloped body on tail globe within.

FIGS. 10-15.—*Cercaria mitocerca*

FIG. 10.—Ventral view of body showing main features.
FIG. 11.—Ventral view showing spherical cell-like bodies after collapse of excretory bladder under pressure.
FIG. 12.—Tail appendage showing three definite divisions.
FIG. 13.—Proximal vesicle of tail globe showing thick walls.
FIG. 14.—Surface of tail globe during contraction showing fissures.
FIG. 15.—Sporocyst showing typical shape.

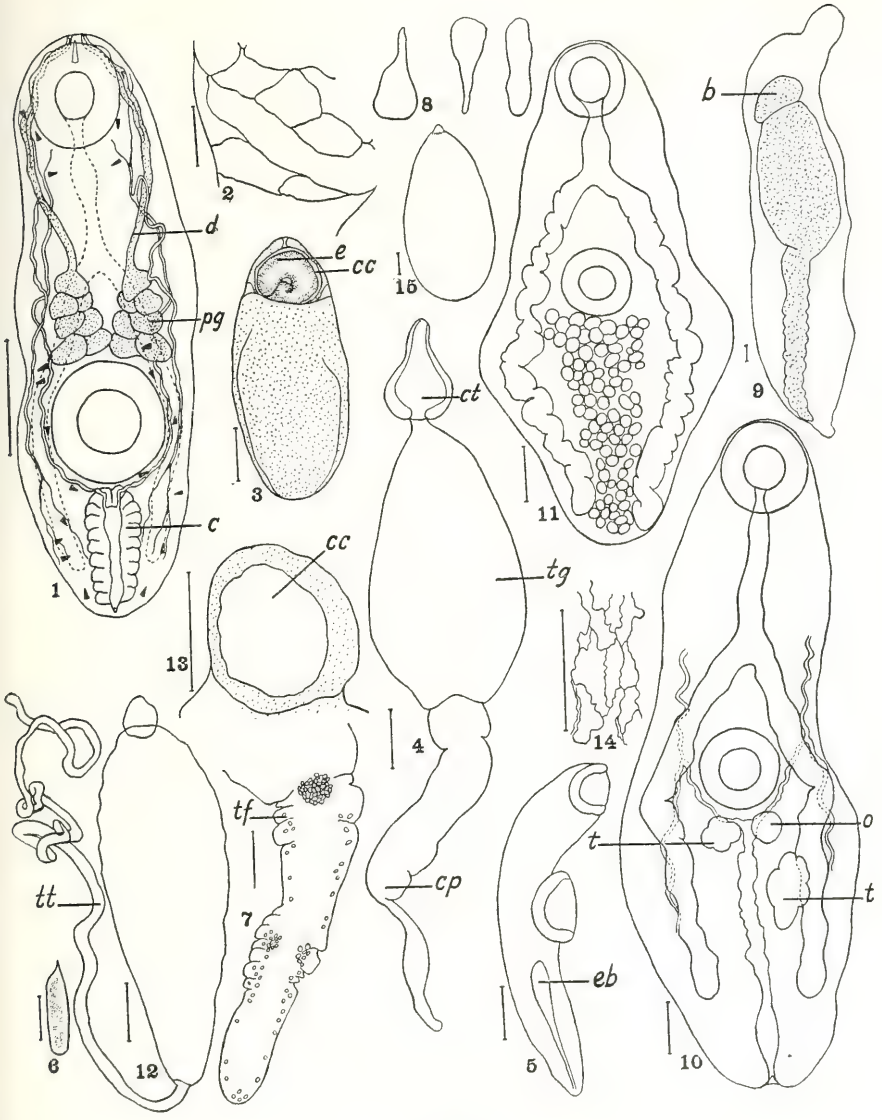

PLATE I

PLATE II

Note.—Figs. 19, 31, and 32 are semi-diagrammatic drawings; scales for all other figures represent 0.1 mm.

FIGS. 16-19.—*Leucochloridium problematicum*

FIG. 16.—Ventral view, showing principle branches of excretory system.
FIG. 17.—Banded sporocyst from the snail's tentical.
FIG. 18.—Body together with gelatinous sheath surrounding it, while subjected to strong pressure.
FIG. 19.—Side view of same showing connections of suckers to outside.

FIGS. 20-27.—*Cercaria urbanensis*

FIG. 20.—Dorsal view, showing main structures of body.
FIG. 21.—Early stage of encystment immediately after loss of the tail.
FIG. 22.—Much later stage of encystment still showing region of tail attachment.
FIG. 23.—The worm about forty-eight hours after encystment.
FIG. 24.—Redia showing complete digestive cecum.
FIG. 25.—Characteristic shape of old redia.
FIG. 26.—Young redia with cercariae in various stages of development.
FIG. 27.—Cercaria in an early stage of development; taken from redia.

FIGS. 28-32.—*Cercaria trivolvis*

FIG. 28.—Dorsal view of the worm with excretory tubules and cystogenous glands shown on alternate sides.
FIG. 29.—Mature redia showing digestive cecum and birth pore.
FIG. 30.—Redia showing posterior locomotor appendages and anterior collar.
FIG. 31.—End of tail showing the small distal body only partially invaginated; semi-diagrammatic.
FIG. 32.—End of tail showing the distal body protruding completely; semi-diagrammatic.

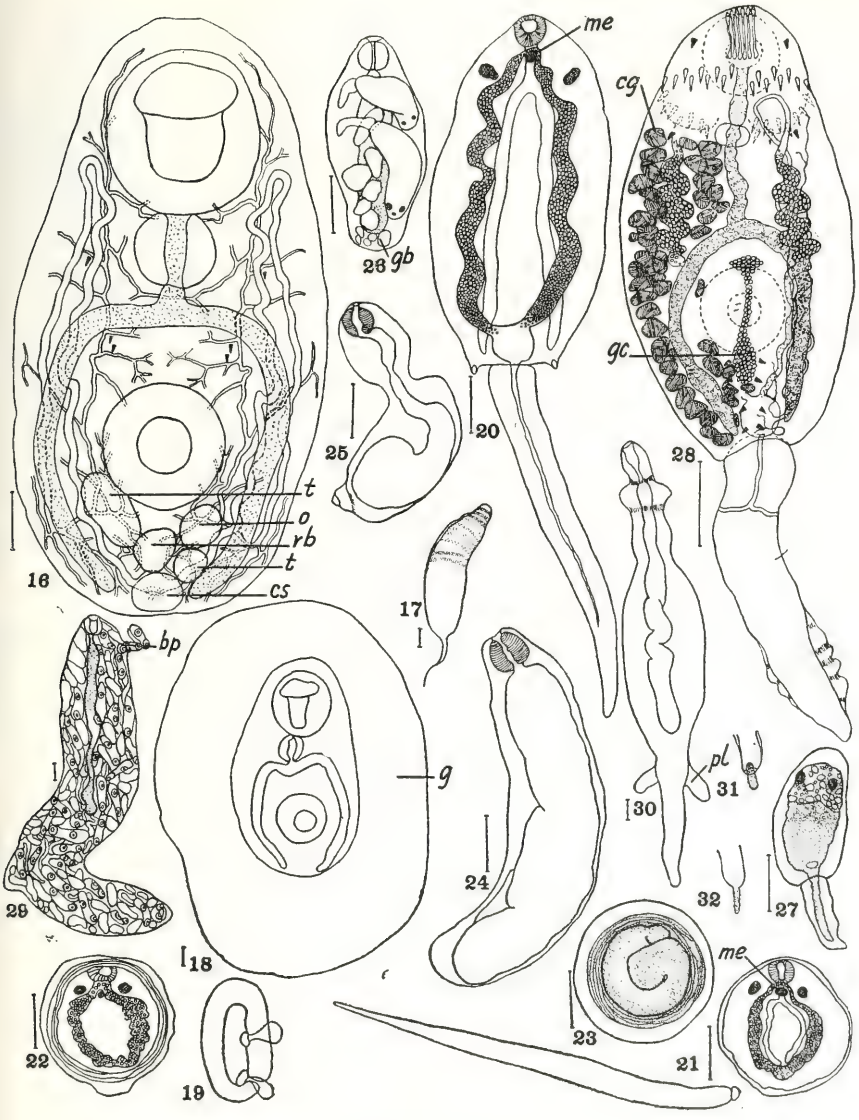
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PLATE II

PLATE III

Note.—Figs. 34 and 48 are semi-diagrammatic drawings; scales for Figs. 39, 43, and 44 represent 0.01 mm.; scales for Figs. 41, 42, 47, 49, and 52 represent 0.05 mm.; scales for all other figures represent 0.1 mm.

FIGS. 33-34.—*Cercaria trivolvis*

FIG. 33.—Redia showing posterior appendages and withdrawn anterior end.
FIG. 34.—Nuclei of tail under very strong pressure.

FIGS. 35-40.—*Cercaria mesotyphla*

FIG. 35.—Ventral view of body.
FIG. 36.—Ventral view showing complete excretory system.
FIG. 37.—Mass of sporocysts in the liver tissue.
FIG. 38.—One end of a sporocyst enlarged to show cercariae within.
FIG. 39.—Dorsal view of stylet, showing its globular base.
FIG. 40.—Sagittal section showing germinal masses dorsal to acetabulum.

FIGS. 41-46.—*Cercaria cystorhysa*

FIG. 41.—Ventral view of body; dorsally located stylet shown with solid outline; body contracted.
FIG. 42.—Ventral view showing main branches of excretory system; extended.
FIG. 43.—Dorsal view of stylet, showing lateral shoulders.
FIG. 44.—Tail under strong pressure and neutral red, showing nuclei and caudal hairs.
FIG. 45.—Sporocyst containing cercariae in various stages of development.
FIG. 46.—Mass of sporocysts attached to the liver tissue of the snail.

FIGS. 47-51.—*Cercaria meniscadena*

FIG. 47.—Ventral view with principle structures shown.
FIG. 48.—Contracted tail showing lateral folds; semi-diagrammatic.
FIG. 49.—Sporocyst with developing cercariae.
FIG. 50.—Sporocyst showing characteristic knobs of older forms.
FIG. 51.—Sporocyst with more pronounced knob.

FIG. 52.—*Cercaria cyclica*

FIG. 52.—Ventral view of the body showing penetration apparatus.

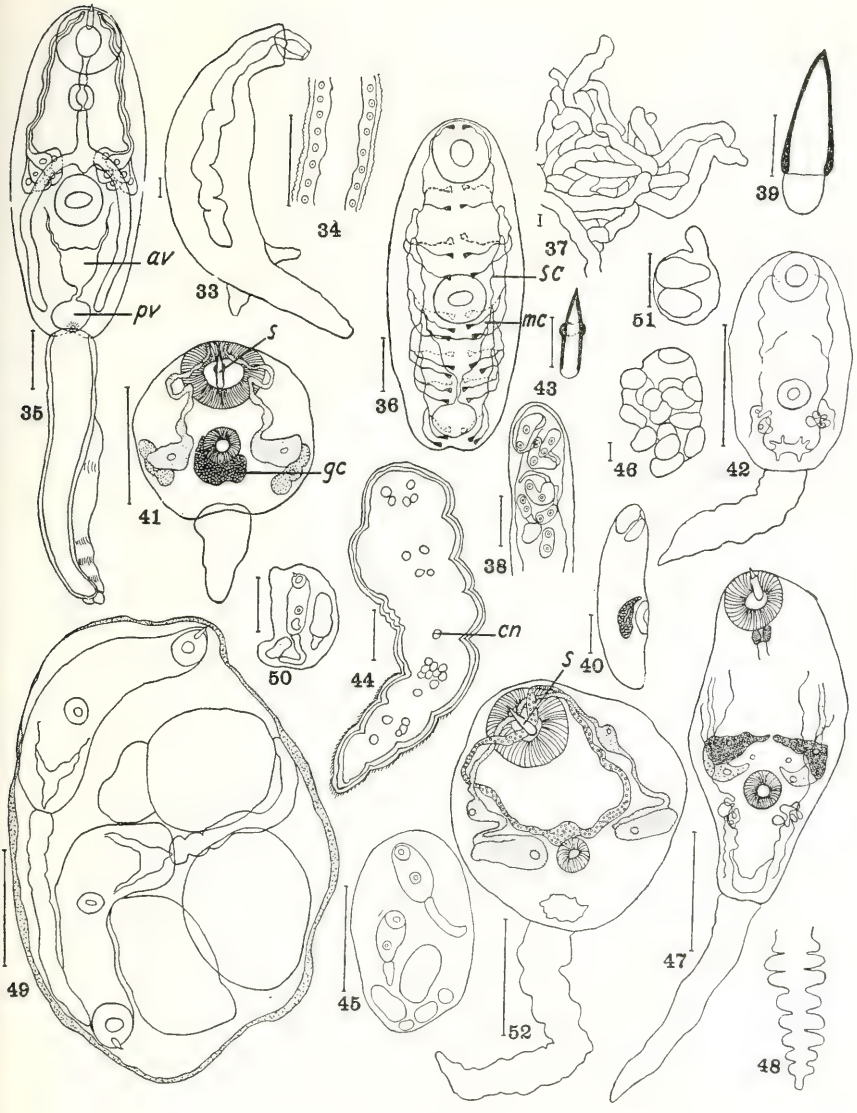
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PLATE III

PLATE IV

Note.—Fig. 57 is a semi-diagrammatic drawing; scales for Figs. 56, 62, 63, and 67 represent 0.01 mm.; scales for Figs. 55, 58, 61, 66, and 68 represent 0.1 mm.; scales for all other figures represent 0.05 mm.

FIG. 53.—*Cercaria cyclica*

FIG. 53.—Ventral view showing main tubules of excretory system.

FIGS. 54-59.—*Cercaria acanthocoela*

FIG. 54.—Ventral view of body.
FIG. 55.—Lateral view of body under no pressure.
FIG. 56.—Dorsal view of stylet showing lateral projections.
FIG. 57.—Various shapes assumed by excretory bladder during life; semi-diagrammatic.
FIG. 58.—Sporocyst showing typical shape; cercariae and germ balls within.
FIG. 59.—Encysted individual showing distension of bladder by granules.

FIGS. 60-65.—*Cercaria tricystica*

FIG. 60.—Dorsal view of body, with suckers shown in broken lines.
FIG. 61.—Ventral view with penetration ducts showing.
FIG. 62.—Dorsal view of stylet showing soft base.
FIG. 63.—Lateral view of same stylet.
FIG. 64.—Tail treated with neutral red to show nuclei.
FIG. 65.—Sporocyst with typical elongate-oval shape.

FIGS. 66-68.—*Cercaria cystonchnoides*

FIG. 66.—Contracted tail showing central lumen.
FIG. 67.—Dorsal view of stylet showing lateral swellings.
FIG. 68.—Lateral view of body when greatly extended during movement; very little pressure.

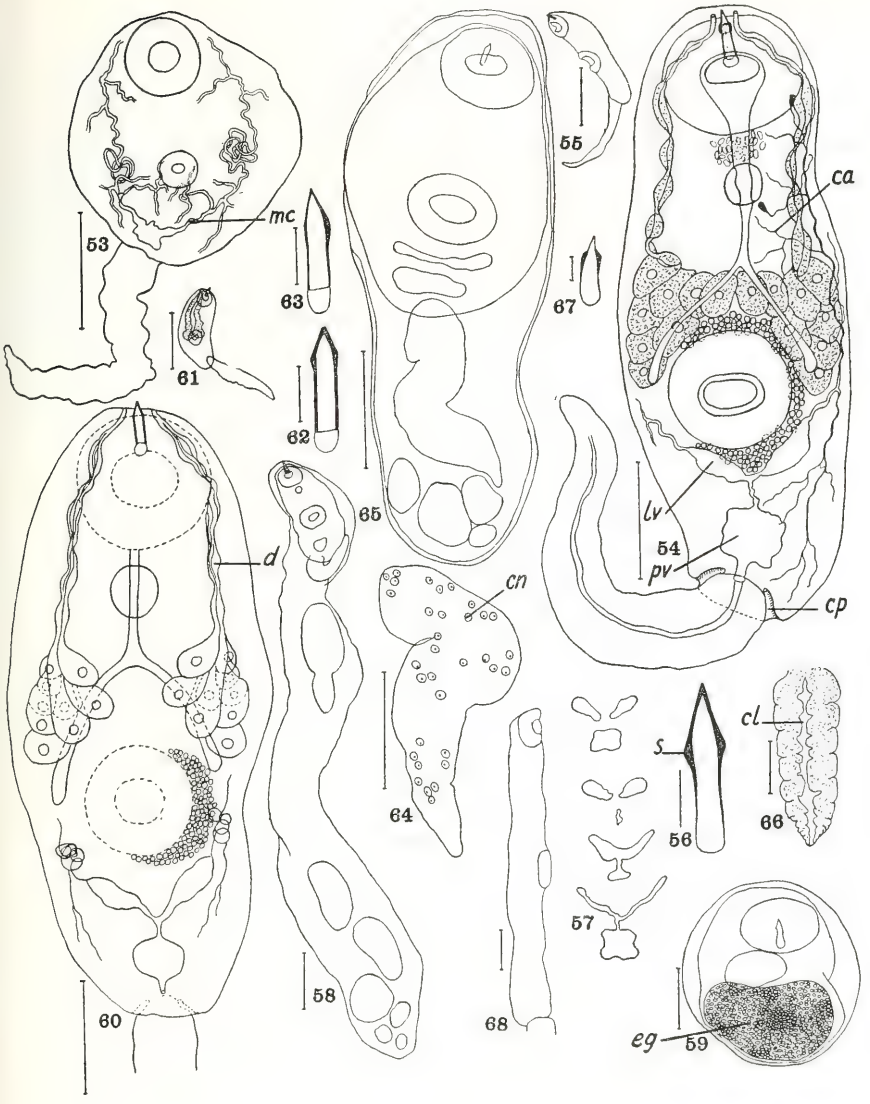
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PLATE IV

PLATE V

Note.—Scales of Figs. 72 and 76 represent 0.01 mm.; scales for Figs. 71 and 74 represent 0.05 mm.; scales for all other figures represent 0.1 mm.

FIGS. 69-70.—*Cercaria cystonchnoides*

FIG. 69.—Dorsal view of body showing complete excretory system.
FIG. 70.—Sporocyst showing typical terminal knobs.

FIGS. 71-73.—*Cercaria steganocoela*

FIG. 71.—Dorsal view of body.
FIG. 72.—View of stylet when turned slightly on its side.
FIG. 73.—Drawing showing filiform sporocyst with various stages of cercariae within.

FIGS. 74-76.—*Cercaria pachycystata*

FIG. 74.—Dorsal view of the body.
FIG. 75.—Mass of sporocysts in the liver tissue.
FIG. 76.—Top view of stylet, showing soft, globular base.

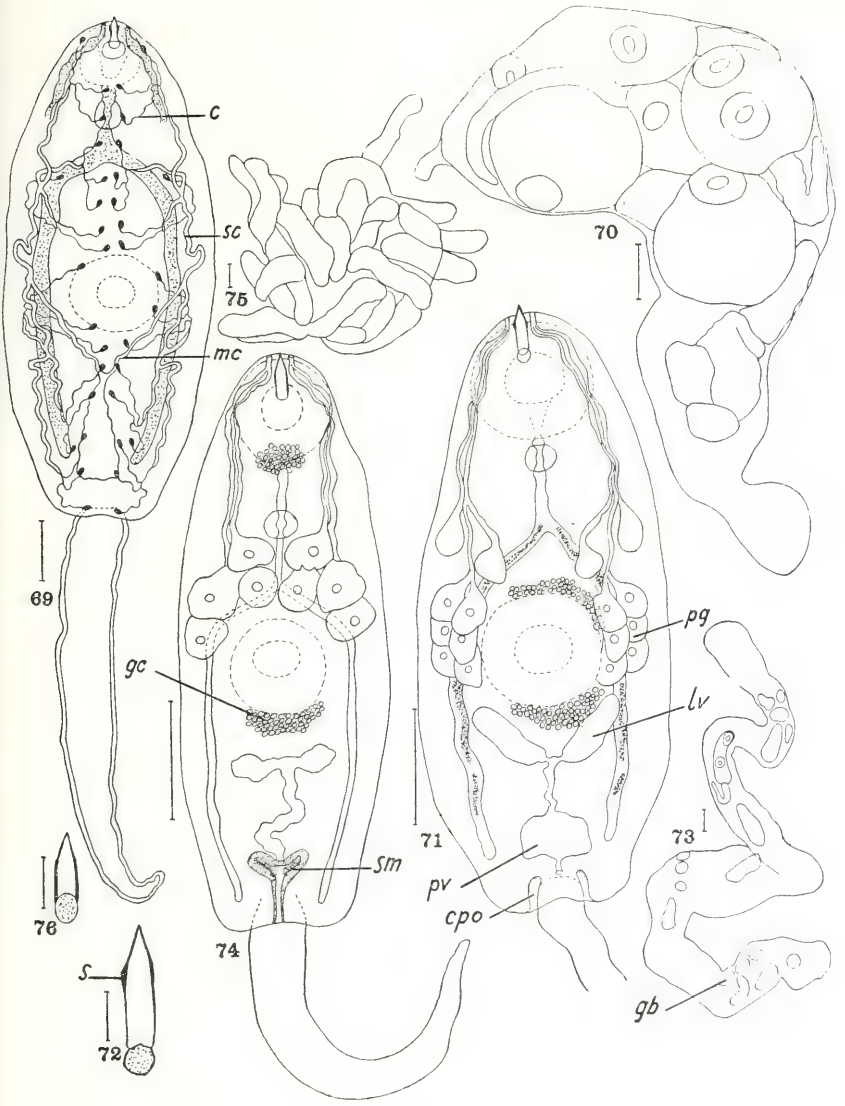

PLATE V

PLATE VI

Note.—The scale for Fig. 87 represents 0.01 mm.; scales for Figs. 79, 80, 82, 85, and 88 represent 0.1 mm.; scales for all other figures represent 0.05 mm.

FIG. 77.—*Cercaria pachycystata*

FIG. 77.—Dorsal view of body to show branches of excretory system in posterior regions of the body.

FIGS. 78-80.—*Cercaria tridena*

FIG. 78.—Dorsal view of the body.
FIG. 79.—Lateral view of the body under no pressure.
FIG. 80.—Sporocyst showing one encysted individual.

FIGS. 81-87.—*Cercaria wardi*

FIG. 81.—Lateral view of the body with the eye-spots flattened by pressure.
FIG. 82.—Tail, showing fin-folds, striations in furcae, and caudal excretory tubule.
FIG. 83.—Furca, showing rayed fin-folds in their dorsal and ventral positions.
FIG. 84.—Lateral view of body, showing complete excretory system.
FIG. 85.—Section of a sporocyst showing developing germ balls and cercariae.
FIG. 86.—Anterior end of body showing dorsal view; also showing spined crown, pyriform anterior organ, digestive tract, and eyes.
FIG. 87.—Greatly magnified view of a caudal flame cell immediately after movement has ceased, showing striations.

FIG. 88.—*Cercaria pteractinota*

FIG. 88.—Dorsal view of body showing eye-spots and the large branches of the excretory system.

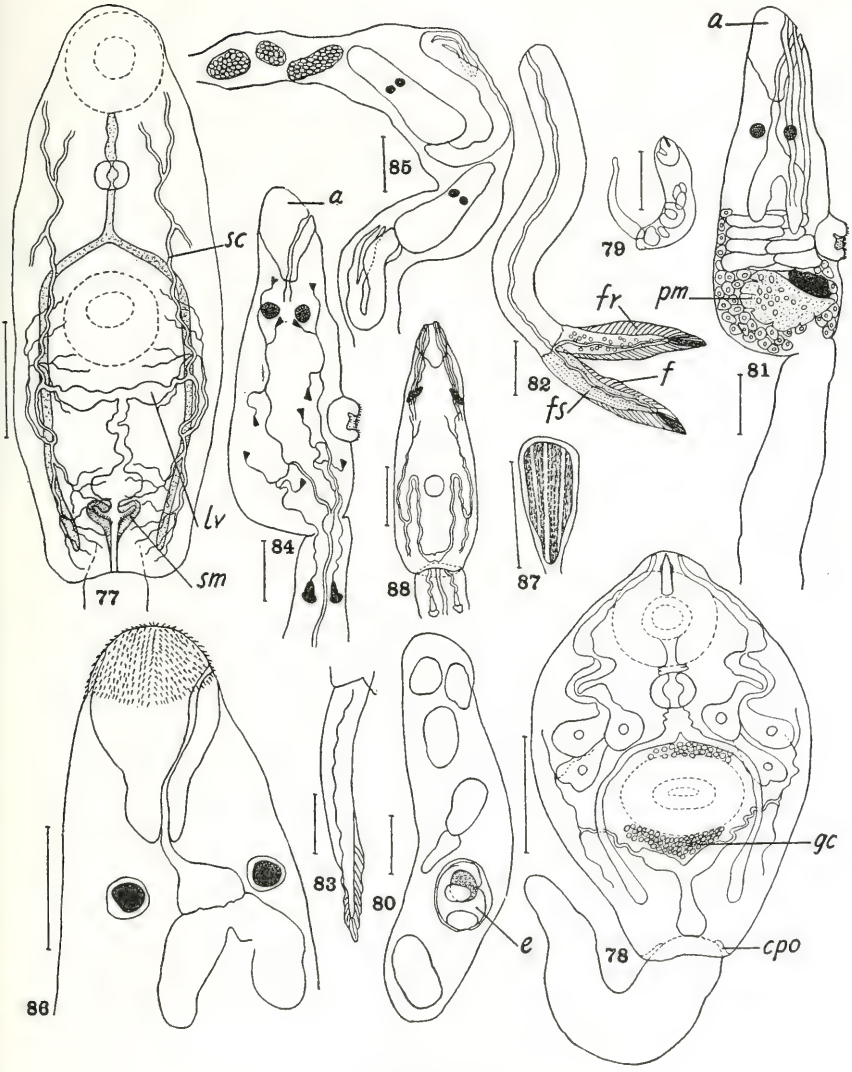

PLATE VI

PLATE VII

Note.—Fig. 94 after original by Faust; Fig. 99 after original by H. M. Miller; scales for Figs. 89, 92, and 98 represent 0.1 mm.; scales for all other figures represent 0.05 mm.

FIGS. 89-93.—*Cercaria pteractinota*

FIG. 89.—Portion of sporocyst showing developing cercariae and germ balls.
FIG. 90.—Furca, showing the rays of the fin-fold.
FIG. 91.—Dorsal view of body showing eyes and the other six principle pigment masses; other pigment not shown. Also the pyriform sucker and crown of spines are shown.
FIG. 92.—Dorsal view showing the entire cercaria.
FIG. 93.—Lateral view to show position of numerous penetration glands and the germinal masses.

FIG. 94.—*Cercaria gigas*

FIG. 94.—Dorsal view of cercaria; after original of Faust; × 125

FIGS. 95-98.—*Cercaria hamata*

FIG. 95.—Dorsal view of body, showing penetration glands, germ masses, digestive tract and complete excretory system.
FIG. 96.—Tail-stem showing sensory hairs and caudal bodies.
FIG. 97.—Furca showing central lumen and small furcal rod.
FIG. 98.—View of cercaria, showing relations of body, tail-stem, and furcae.

FIG. 99.—*Cercaria multicellulata*

FIG. 99.—Dorsal view; after original of Miller; × 500

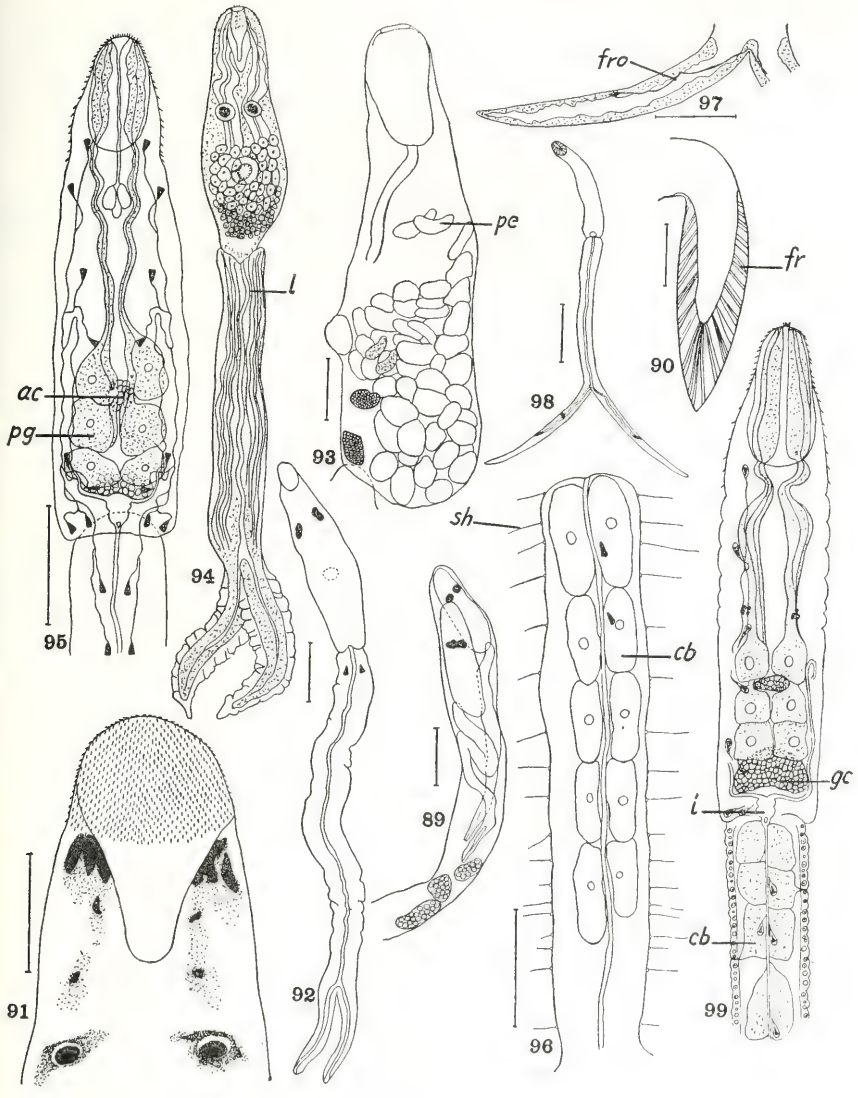

PLATE VII

PLATE VIII

Note.—Fig. 100 after original by Cort and Brooks; scales for Figs. 101, 103, and 108 represent 0.1 mm.; scales for all other figures represent 0.05 mm.

FIGS. 100-101.—*Cercaria bessiae*

FIG. 100.—Dorsal view of Cercaria; after original of Cort and Brooks; semi-diagrammatic drawing.

FIG. 101.—Section of filiform sporocyst.

FIGS. 102-104.—*Cercaria furcalineata*

FIG. 102.—Dorsal view of body and anterior portion of tail-stem.

FIG. 103.—Entire cercaria without pressure, to show relation of body, tail-stem, and furcae.

FIG. 104.—Enlarged furca showing furcal striations and position of nuclei.

FIGS. 105-108.—*Cercaria louisiana*

FIG. 105.—Dorsal view of body showing anterior crown of spines, oval anterior organ, eye-spots, penetration glands, germinal mass, rudimentary sucker, and excretory bladder.

FIG. 106.—Tail-stem, showing position of muscle bands and nuclei after neutral red has been added.

FIG. 107.—Furca, showing fin-folds, nuclei, and position of muscle bands.

FIG. 108.—Entire cercaria showing relations of body, tail-stem, and furcae; drawn without the application of pressure.

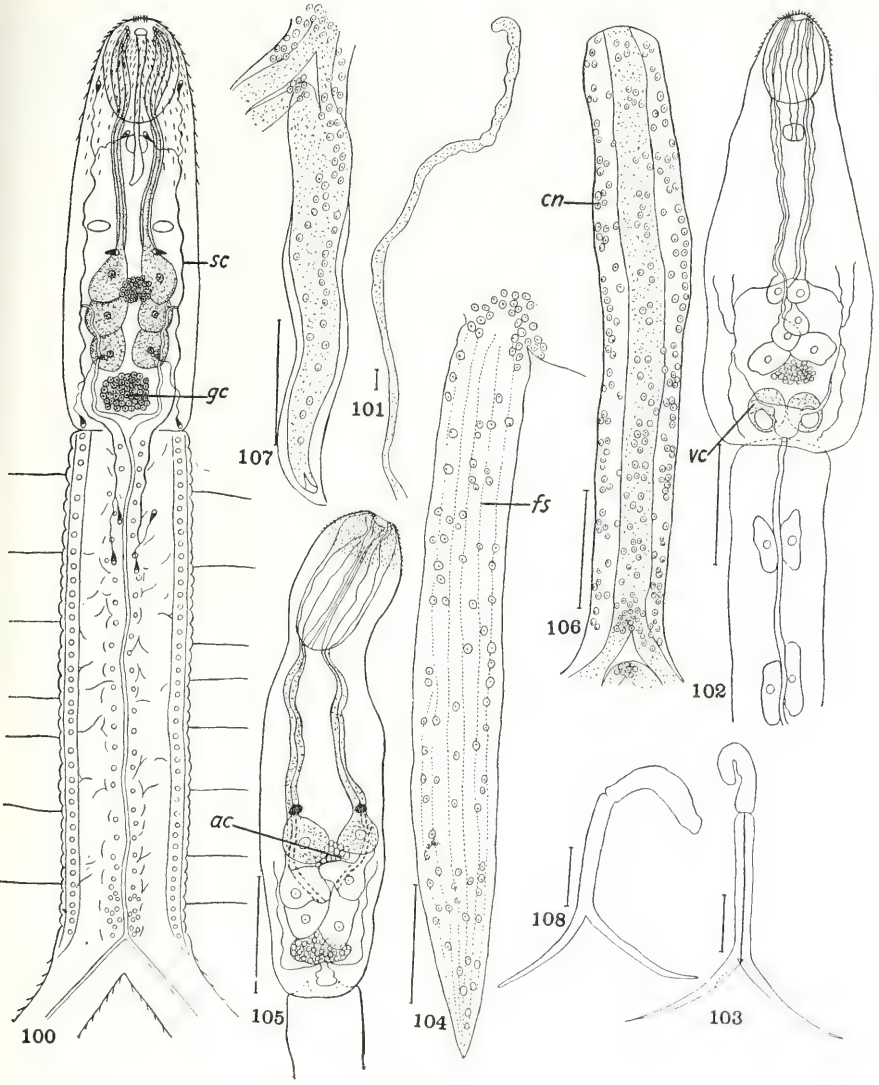

PLATE VIII

INDEX